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THE UNIVERSITY OF ALBERTA

MOVEMENTS OF COYOTES IN SOUTHWESTERN MANITOBA

by

H. DEAN CLUFF ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1992

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled MOVEMENTS OF COYOTES IN SOUTHWESTERN MANITOBA submitted by H. DEAN CLUFF in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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ABSTRACT

Coyotes (*Canis latrans*) were radio-collared in southwestern Manitoba, 1988-1990 to investigate their movements and home range size relative to biological attraction sites. I determined the influence of estimation techniques on measures of home range size, checked for differences in parental care during the rearing of pups in summer, and determined the impact of carcass sites on coyotes in winter. I compared measures of home range size for the same coyote using the 95% minimum convex polygon and the 95% harmonic mean methods. I examined paired estimates where I used different degrees of statistical independence of locations. Home range sizes estimated with autocorrelated locations were not significantly different from those estimated with independent locations. However, harmonic mean estimates were 2- to 5-times greater than estimates from the minimum convex polygon method. A percent area polygon of a non-statistical home range estimator may not be comparable to a probability ellipse of a statistical estimator of the same percentage.

Summer home ranges of denning coyotes were about half the area enclosed by composite home ranges but this area appeared to increase as the summer progressed. Adult males and females differed in time spent at the den site. Males averaged 40% of their time at the den throughout the summer. Females spent about 60% of their time at the den during May and June but did not differ from males in July and August Activity of adults increased in mid- to late afternoon as the summer progressed. Pups were left unattended for 42% and 48% of the time in June and in July/August respectively. Parents were more likely to leave pups alone during the night.

Coyotes were also monitored at carcass sites that I provided in winter to examine the influence of carcasses on coyote movements and home range size. Coyotes visited all carcass sites but carcass use was less than expected. Coyotes appeared initially wary of carcasses that I had introduced. Consumption of carcasses occurred later at these sites than where I had added food to sites that had livestock carcasses dumped there in previous years. I did not detect any differences in carcass use by resident coyotes when I introduced carcasses to the home range center or edge. Use of carcasses at the home range edge also depended on the extent of use from coyotes thought to occupy areas adjacent to the home range that received my food additions. Carcass sites used by resident coyotes may have shifted the harmonic mean activity center towards the site for 2 of 8 monitored coyotes but carcass use did not appear to significantly alter home range size. Therefore, carcasses may not influence home range use of coyotes as initially thought.

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This study was part of the Large Mammal Systems Study conducted under the Man and Biosphere program and coordinated by the Canadian Wildlife Service and the Canadian Parks Service. Their commitment to long-term monitoring and research in the Riding Mountain National Park biosphere has been welcome. Without their combined effort, this study would not have been possible. Logistical support provided by the Canadian Wildlife Service, Western and Northern Region, Environment Canada in Edmonton was instrumental to this project. Their patience and flexibility to accommodate my requests in the field have not been forgotten. I also thank the Department of Zoology, University of Alberta, for providing financial support while I was in the field and on campus. I gratefully acknowledge the support of Manitoba CareerStart and the Unemployment Insurance Job Creation Section 38 Program of the Unemployment and Immigration Commission of Canada whose funding provided me with assistants to augment my efforts at monitoring coyotes. The Canadian Circumpolar Institute (formerly the Boreal Institute for Northern Studies) provided much needed funding to initiate the study. Their grants to me and L.N. Carbyn are much appreciated.

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Finally, I an indebted to my parents for their unrelenting support in my endeavours without whom I could not have pursued my interest in wildlife. To this end, I am truly grateful and I dedicate this thesis to them.

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CHAPTER 1

GENERAL INTRODUCTION

Although coyotes have received considerable research attention, much of the effort has been directed towards their control or destruction. Ever since Europeans first settled western North America, their encounters with coyotes have often been fatal for this mid-sized canid (Young and Jackson 1951). The attitude that carnivorous animals were threats to wildlife and domestic animals and must be systematically destroyed has prevailed for some time (Connolly and Longhurst 1975). The ability of coyotes to endure this onslaught of persecution has served to affirm their durability (Andelt 1987, Voigt and Berg 1987). Perhaps as a result of ineffectual population control (Voigt and Berg 1987), the last three decades have seen more research effort directed towards understanding the ecology and behavior of coyotes (Bekoff 1982).

Coyotes are variable in their ecology and behavior throughout their geographical range. For example, understanding the underlying mechanisms for home ranges of coyotes, parental care of young, and responses of coyotes to changes in their food supply has proven difficult partly because variation is introduced from many sources. Variation we observe in ecology is due to ecological conditions, individuals, and the techniques we use to acquire data. Variation introduced with techniques merely confounds the variation we seek to understand. However, it is also clear that individual variation in response to identical ecological conditions remains large. Consequently, manipulative experiments in the field are necessary to factor out the relevant variables and provide reliable knowledge (Romesburg 1981, White and Garrot 1990).

Coyotes have expanded their range from the time of European settlement (Bekoff 1977, Voigt and Berg 1987) while showing a persistent ability to survive in a variety of habitats (*e.g.*, Murray and Boutin 1991). Extensive environmental change from human activity has likely contributed to the range expansion of coyotes but concomitantly this increase in range has increased encounters between coyotes and humans. Although encounters are usually benign, reports of aggressive behavior towards humans by coyotes have increased (Howell 1982, Carbyn 1989, Dawson 1991). Many of these aggressive encounters towards humans by coyotes have occurred when coyotes were involved in pup rearing (Carbyn 1989). Explanations of such behavior have been attributed to food stress (Carbyn 1989) or loss of fear to humans by coyotes, the latter often due to humans feeding wildlife in park settings (Carbyn 1989). This problem has often been alleviated by the removal of the offending individuals or destruction of the den site and the offspring ('denning') whenever the den is found (*e.g.*, Young and Dobyns 1937, Till and Knowlton 1983). However, understanding the behavior of denning coyotes and the relationship with their food supply may reduce the potential for conflicts with humans, especially in protected areas where unnecessary destruction of wildlife is discouraged.

Few studies have investigated the role of food supply in coyote ecology (*e.g.*, Clark 1972, Todd and Keith 1976, Hoffman 1979, Mills and Knowlton 1991) while only one (Todd and Keith 1976) has manipulated the food supply. However, these studies have only considered the influence of winter food resources while ignoring the summer season, probably because summer is considered a time where food is relatively abundant. With the exception of wolves (*Canis lupus*) (Mech 1977), winter is the period that food stress is thought to occur while summers should yield abundant prey for predators. Consequently, summer food studies of coyotes seem only to document what coyotes have eaten during this period. However, denning adult coyotes, faced with feeding a litter of 4-6 pups or more, may exact a demanding role of provider for the parents, at least during some periods. Carbyn (1989) suggested this possibility to explain the increased aggression to humans by coyotes in July. Pups, at this time, may be in transition from relying on adults for food to acquiring food on their own. Therefore, July may be the time of greatest nutritional stress for denning adults and they must therefore increase their foraging activity to meet this demand.

Because adult coyotes may spend about half their time attending pups until these pups are at least nine weeks of age (Harrison 1983), foraging effort may require much of the remaining time. If foraging efficiency is paramount then it should manifest itself in the movements and behavior of denning adult coyotes.

In this study, I examined relationships between coyotes involved in pup-rearing activities during summer and their use of carcasses in winter. I asked the following two questions: Does the activity of denning adult coyotes change over the summer with the development of pups, and what is the extent of use of carcasses available to coyotes in winter? I also tried to show that techniques used to estimate home range sizes of coyotes and the procedures I used to manipulate food supply available to coyotes contribute significantly to the observed variation in home range size.

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CHAPTER 2

EFFECTS OF AUTOCORRELATION AND ESTIMATION TECHNIQUES ON HOME RANGE SIZES OF COYOTES IN SOUTHWESTERN MANITOBA

INTRODUCTION

Home ranges of coyotes have been documented extensively throughout their geographic range (see Laundré and Keller 1984, Andelt 1987 for reviews). Estimates of home range size vary widely from 4-5 km^2 in Texas (Andelt 1985) to over 100 km^2 in Washington (Springer 1982) causing frustration among researchers because few generalizations can be made (Andelt 1987). Variation in home range size reflects variation in at least three factors; ecological conditions, individuals, and the techniques used to estimate the home range. Variation in home range size resulting from individuals responding to ecological conditions such as food supply and intraspecific competition is what we seek to understand. Variation introduced from home range estimation techniques simply confounds the role that ecological factors play. Variation resulting from techniques has contributed all too much to the overall variation we observe in coyote home range sizes (Laundré and Keller 1984).

There is no definitive method of estimating home range size nor is there an apparent concensus for the preferred technique (Mohr and Stumpf 1966, Jennrich and Turner 1969, Van Winkle 1975, Ford and Krumme 1979, Macdonald et al. 1980, Schoener 1981, Anderson 1982, Cheeseman and Mitson 1982, Samuel and Garton 1985, Harris et al. 1990, White and Garrott 1990). In the last decade efforts have been directed to investigating the statistical properties of some commonly used home range models (Bekoff and Mech 1984, Boulanger and White 1990). Through computer simulations some models have been tested against fixed areas from a known distribution of points and have shown that use of different home range estimators may contribute significantly to observed variation (Boulanger and White 1990).

Approaches to estimating home ranges can be categorized as statistical (probabilistic) or non-statistical. Statistical methods attempt to assess an individual's probability of occurrence at each point in space (Van Winkle 1975, Harris et al. 1990) while non-statistical methods deal only with the actual locations (White and Garrott 1990). The harmonic mean estimate (Dixon and Chapman 1980) and the minimum convex polygon estimate (Mohr 1947) are examples of the statistical and non-statistical models, respectively. Both methods are commonly used and are supported on most computer software packages that estimate home range (see White and Garrott 1990:173 for a list). The minimum convex polygon (MCP) method is one of the oldest and most common among methods that delimit home range (Mohr 1947, Harris et al. 1990). A range boundary is constructed by connecting the outermost locations to form a convex polygon. The home range size is the area enclosed by the polygon. Typically, the outer 5% of the locations (or fixes) are omitted as a way of discounting outlying locations. The harmonic mean (HM) method outlined by Dixon and Chapman (1980) and later modified by Spencer and Barrett (1984), calculates one or more centers of activity that are used to generate activity area isopleths. Consequently, range configurations relate directly to the frequency of occurrence of an individual within its home range (Dixon and Chapman 1980, Harris et al. 1990, White and Garrott 1990). Home range areas are estimated by calculating isopleths within which a given proportion of locations are found (Harris et al. 1990). Normally, 75% (*e.g.*, Windberg and Knowlton 1988) or 95% (*e.g.*, Cresswell and Harris 1988) isopleths are calculated.

Both of the above methods share the assumption that all locations must be statistically independent (not autocorrelated). Because tracking data are at least 3-dimensional, having coordinates in space and time (x,y,t), the closer in time two locations are taken, the less likely they are to be statistically independent (White and

Garrott 1990). Simulation procedures have shown that positive autocorrelation (usually from sampling over a short time interval) results in an underestimation of home range size (Swihart and Slade 1985a).

Both HM and MCP methods are also sensitive to the sample size of locations used in the home range estimate. Small sample sizes are generally restricted in time that is insufficient to allow the individual to traverse its effective home range area. On the other hand, increasing the number of radio-fixes collected within the same time period may introduce autocorrelation. Acquiring a large data set with statistically independent relocations might occur over a time period that incorporates a shift in an animal's movement behavior and exaggerate the home range estimate. Consequently, the interactions between sample size and time period must receive careful consideration in any investigation of home range size.

Field data are inappropriate for statistical tests that evaluate bias and precision of home range estimators because there is virtually no way of knowing the actual home range (at least for coyotes) and field telemetry data cannot be truly replicated (Boulanger and White 1990). However, one can evaluate the variation introduced by estimation procedures by using a single set of field data collected on the same individual. By doing so, ecological and individual factors determining home range size are held constant. To my knowledge this has not been done.

In this study, I compared the effects of both estimation technique and autocorrelation on home range size estimates using a series of locations for coyotes in southwestern Manitoba. I controlled for individual and ecological effects by comparing each of the above factors for individual animals.

METHODS

1. STUDY AREA

Radio-collared coyotes were monitored in, and immediately south of, Riding Mountain National Park (RMNP) in southwestern Manitoba, Canada (50° 40' lat., 100° 10' long.). The study area encompassed a 150 km^2 region consisting of aspen parkland dominated by agriculture (see Appendix 1 for a detailed description of the study area). A network of roadways outside RMNP allowed vehicle access for monitoring coyotes. Access inside the park was more restricted, but mostly in winter when some roads were not ploughed of snow.

2. DATA SETS USED FOR ANALYSIS

Radio-locations were obtained for 16 coyotes from December 1988 to August 1989 and from December 1989 to August 1990. Locations were estimated by triangulation from bearings obtained by a hand-held antenna from a ground vehicle. Normally three bearings were taken for each location estimate although locations based on two or four bearings were also used. The ad hoc method (Nams and Boutin 1991) was used to initially reject locations considered too imprecise. The error triangle technique (Nams and Boutin 1991) formed the basis of estimating an individual's location although the probability of the estimate containing the true location could not be determined (Nams and Boutin 1991). However, reference transmitters at known locations were used to estimate the accuracy and precision of the triangulation procedure using the maximum likelihood estimator (Lenth 1981) provided in the LOCATE II program (Nams 1990). Based on these reference transmitters, bearing error was estimated at ±2.0°.

Coyotes were usually monitored three times a day in winter at approximately eight hour intervals. In summer, focal coyotes were monitored once every hour, 12-16 hours/day, for 2-week periods in June and in July. At other times location attempts were made 1-2 times a day. I separated locations for each radio-collared coyote into winter (Dec-Mar) and summer (May-Aug) periods within years because home range use by coyotes is known to change over the course of a year (Smith et al. 1981, Laundré and Keller 1984). I used the program package HOME RANGE (Ackerman et al. 1990) to measure autocorrelation, identify outliers, determine home range, and plot results. The HOME RANGE package identifies outliers as significant by a binomial statistical confidence interval test (Ackerman et al. 1990). However, seven estimates produced by the harmonic mean method were 1.5 to 8 times the average (39.7 km^2) because 1-3 points that were located well away from the centre of the home range. In these cases, I removed those points and recalculated the home range size. For all home range size estimates, I followed convention and reduced the potential influence of infrequent excursions outside the 'normal' home range by removing the outermost 5% of locations and reported the 95% contour level of the estimated home range area.

I selected data sets of those coyotes for which I had at least 30 locations to compare home range sizes. I chose 30 as the minimum because I wanted to have home range estimates over a reasonably comparable time frame for different sampling intensities when sample size was to be held constant. For example, for this study I accepted a home range estimate calculated from three locations per individual per day over a 10 day period as comparable to a once-a-day sampling over 30 days. Also, I used a sample size small enough to approximate realistic field conditions where logistics and unforeseen circumstances may limit data collection efforts. I expected that sample sizes below 30, however, might lead to spurious conclusions for this analysis.

3. CONSIDERATIONS FOR ANALYSIS

3.1 Direct Comparison

I compared home range size estimates of coyotes from the HM and MCP methods using the entire, unmanipulated data sets for a given season although many assumptions of each method would be violated. I removed outliers identified by the HOME RANGE package and compared the resulting home range size estimates with those not having outliers removed. I ignored subsequent outliers that the HOME RANGE package identified after I had removed the initial outliers because the software is actually evaluating a different set of data. I used the paired sample *t*-test to test for significant differences between paired comparisons of home range sizes.

3.2 Autocorrelation

I used Swihart and Slade's (1985b) t^2/r^2 ratio (modified from Schoener 1981) and ψ (psi) (Swihart and Slade 1985a) and γ (gamma) (Swihart and Slade 1986) provided in the HOME RANGE program to indicate potential autocorrelation among successive locations during summer and winter monitoring periods. The t^2/r^2 ratio compares the mean squared distance between successive observations (t^2) to the mean squared distance of each observation from the center of activity (r^2). A t^2/r^2 of 2.0 is expected if all observations are statistically independent (Ackerman et al. 1990). Psi and gamma are scalar bivariate measures of autocorrelation derived from Schoener (1981). Psi differs from gamma in that it also considers cross correlations (Swihart and Slade 1985b, 1986). However, I only considered the t^2/r^2 ratio for *t*-tests of significant departures ($\alpha < 0.05$) from independence because of its support in the HOME RANGE package and the ratio's comparable agreement with ψ and γ for the data I examined. A one-tailed test was used because I was only interested in positive autocorrelation (*e.g.*, $t^2/r^2 < 2.0$). Therefore, I tested the null hypothesis that observations were independent or overdispersed ($t^2/r^2 \geq 2.0$).

Several minimum times between successive locations (*e.g.*, 4, 8, 12, 16, 20, and 24 hrs) were tested to determine the minimum time interval to achieve independence of observations. This 'time to independence' (Swihart and Slade 1985b) was used to eliminate any successive observations within this time period before estimating home range size without autocorrelated locations. I considered $\alpha = 0.25$ (Swihart and Slade 1986) in addition to $\alpha = 0.05$ because choosing a large α reduces the probability of a Type II error for the null hypothesis of independence of locations (Swihart and Slade 1985b, 1986).

I compared home range sizes as calculated by the two estimation techniques using both independent and autocorrelated locations. I began testing for autocorrelated data sets with consecutive locations at least eight hours apart and progressed with shorter intervals until the index indicated that the points were autocorrelated. I accepted a data set as independent or autocorrelated when both t^2/r^2 and ψ indicated the data as such. There were three cases of an animal within a season having locations that were not independent even if locations were taken 48 hours apart. I included these cases in a separate analysis because I considered a 2-day interval between successive locations as independent although the t^2/r^2 index suggested otherwise. Consequently, I dismissed the apparent lack of independence as an artifact of methodology because individuals that permanently shift their home range to a new location invalidate the t^2/r^2 ratio by inflating r^2 (Swihart and Slade 1985b). In these three cases, the coyote did not show fidelity to any particular area.

3.3 Autocorrelation and Sample Size

The time frame over which autocorrelated and independent relocations were initially drawn was identical between paired comparisons. However, comparing the influence of autocorrelation on estimates from the two home range methods is complicated by variable sample sizes for subsets of locations. The potential to influence home range size estimates with locations included in one data set but not the other can be significant. Consequently, I chose an equal number of radio-locations from an autocorrelated data set as were present in the data set containing only independent locations. However, exact subsets of autocorrelated and independent locations are not possible because equal sample sizes of autocorrelated locations occur over a smaller time span than when independent. Therefore, I tried to minimize large time differences by randomizing the selection of locations needed for the autocorrelated data set. This procedure minimized the number of autocorrelated locations in any one compressed time span (*e.g.*, 8 locations in 1 day) but still maintained significant autocorrelation for comparison with an independent data set.

For statistical analyses of autocorrelational effects, I used a 3-way randomized block design ANOVA with individual coyotes as the blocking factor and home range estimation method and independence of data as the main effects (SAS Institute Inc. 1987). I used a paired sample *t*-test to extend tests of home range sizes in paired comparisons.

RESULTS

1. SAMPLE SIZES FOR ANALYSES

Of 31 coyotes captured and fitted with radio-collars (see Appendix 2 for capture data), 16 were monitored sufficiently for a direct comparison of home range estimates. Because the same coyotes were monitored for two or more seasons, my sample size effectively increased to 27 'seasonal individuals' for my initial comparison. Subsequent comparisons were reduced to sample sizes of 15 and 18 (Section 3.2) 'seasonal individuals'. This was because data sets of coyotes were selected to satisfy various assumptions of the 2 home range estimators and still have 30 or more locations.

2. INDEPENDENCE OF OBSERVATIONS

There was no one specific time interval after which successive radio-tracking observations could be considered independent. Tests of independence of observations in winter (Table 2-1) showed that a minimum of 12 hours were required between successive locations at the $\alpha = 0.05$ level. At least 16 hours were needed if an $\alpha = 0.25$ level was used (Table 2-1). Complete *t*-test results are provided in Appendix 3 (Tables A3-1, A3-2).

The t^2/r^2 index indicated that coyotes C07, C11, C20 (winter 1990), and C23 required more than 24 hours between successive locations before the locations could be considered statistically independent. However, three of these coyotes (not C11) permanently shifted the location of their home ranges over the winter which would have influenced the test statistic (t^2/r^2). Although coyote C11 showed fidelity to one area, it had a relatively small home range area (5.9 km^2 with locations at least 24 hours apart) and some of the outer points could influence the test statistic in a fashion similar to home range shifts.

Fewer coyotes were available or adequately sampled for tests of independence of successive observations in summer (Table 2-1). Statistical independence ($\alpha \leq 0.05$) was achieved for coyotes C22 and C68 when as little as three or more hours had elapsed. However, consecutive observations for coyotes C04, C17 and C31 were considered autocorrelated even after 24 hours or more separated consecutive locations. Coyotes C04 and C11, however, were denning females and may have relocated their den sites repeatedly, thus changing their activity centres.

3. HARMONIC MEAN AND MINIMUM CONVEX POLYGON ESTIMATORS

3.1 Direct Comparison

Harmonic mean estimates of home range sizes of coyotes at the 95% contour level varied from 8.2 to 123.2 km^2 for 27 seasonal home ranges (Table 2-2). When initial outliers were removed (n = 23) (Ackerman et al. 1990), harmonic mean estimates ranged from 0.2 to 66.4 km^2 (Table 2-2). Not surprisingly, home ranges estimated by the HM method were significantly smaller when outliers were eliminated ($t_{26} = 5.145$, $p < 0.0001$). On average, there was a 5.8-fold decrease in individual home range sizes when outliers were removed although differences were highly variable (S.D. = 11.23-fold, n = 27). In 13 cases, additional outliers were still identified after initial outliers were removed (Table 2-2). However, these were not removed for this or any further analysis as indicated earlier.

Minimum convex polygon estimates (95% contour level) for the same data sets ranged from 3.0 to 44.7 km^2 (Table 2-2). These home range size estimates were 3.1-fold smaller (S.D. = 2.57-fold, n = 27) smaller than HM estimates not having outliers removed ($t_{26} = 6.630$, $p < 0.0001$). Correlation analysis ($r^2 = 0.607$) suggests that a correction factor (HM = -1.859 + 2.622 x MCP) could be used to relate one method to the other (Fig. 2-1a). Harmonic mean estimates with outliers removed were 1.25 times larger (S.D. = 0.77-fold), on average, than MCP estimates (Table 2-2). The correlation between the two methods also improved ($r^2 = 0.829$) when outliers were removed prior to calculating harmonic mean estimates.

3.2 Effect of Autocorrelation

Home range sizes calculated from independent locations only or with autocorrelated locations (Table 2-3) were not significantly different when estimated by either the HM or MCP methods ($F_{1,43} = 0.540$, $p = 0.465$). There was no pattern in the direction of change in home range size estimates based on autocorrelated locations versus independent locations (Fig 2-2). For seasonal home ranges, 10 of 18 HM estimates and eight of 18 MCP estimates were smaller with autocorrelated locations than with independent ones (Table 2-3, Fig. 2-2).

Using statistically independent locations only, home range size estimates reported by the two methods were significantly different ($F_{1,43} = 7399.262$, $p = 0.0001$) with HM estimates averaging 3.8-fold greater (S.D. = 1.96-fold) than MCP estimates. The difference was greater (4.5-fold increase) and more variable (S.D. = 3.18-fold) with autocorrelated locations. Harmonic mean and MCP estimates remained significantly different whether locations were autocorrelated ($t_{17} = 7.541$, $p = 0.0001$) or independent ($t_{17} = 4.450$, $p = 0.0004$). The correlation between the two methods was poor ($r^2 = 0.287$) when independent locations and equal sample sizes were used (Fig. 2-1b).

DISCUSSION

1. Time To Independence

Often radio-equipped animals are monitored intensively, with locations being determined up to several times/hour. The frequency of this will likely increase as technology advances (see Tomkiewicz 1991). While continuous sampling is generally advantageous, certain assumptions that are required for some analyses such as independence of fixes are likely violated. Consequently, a subset of locations that meet the necessary assumptions is usually selected. For home range studies, a filter is used that identifies the 'time to independence', or the time interval at which autocorrelation becomes insignificant (Swihart and Slade 1985a). No time interval has been reported for coyotes that filters radio-locations to achieve independence of locations as assumed for home range size estimates. However, Harrison and Gilbert (1985) used 4.5 hours as a minimum time between locations to calculate mean distances between locations and to avoid oversampling of resting individuals. In my study, locations of radio-collared coyotes were statistically independent in winter after at least 12 hours had elapsed between consecutive locations. The time to independence may be less in summer, possibly because movements away from a den site occur frequently (see Chapter 3) while fidelity to a given area occurs less often in winter.

Studies that employ sequential sampling (Laundré and Keller 1984) should be concerned about autocorrelation unless point sampling (Laundré and Keller 1984) is strongly periodic (*i.e.*, at the same time each day). Point sampling (usually 1-2 times/day) assumes that an adequate time span has elapsed before the next location is estimated although the assumption should always be tested. In many studies that collected data sequentially, it is unclear if the assumption of independence of locations was addressed by the authors (*e.g.*, Andelt 1985, Mills and Knowlton 1991) or was ignored (*e.g.*, Gipson and Sealander 1972, Smith et al. 1981, Bowen 1982, Woodruff and Keller 1982).

In five cases, I found that consecutive locations were considered autocorrelated by the t^2/r^2 index after a 48-hour interval. I expected that most consecutive locations should be independent after 48 hours based on the relative distance between these locations. However these individuals shifted their home range area during a season. Shifts in home range use typically lead to a rejection of the independence assumption because shifts lead to calculation of a new relative centre of activity (Swihart and Slade 1985b). Consequently, r^2 is larger when locations on either side of the shift are considered together than if locations are analyzed separately before and after the shift. It is also possible that one or more outliers may strongly influence the activity centre and the resultant autocorrelation index. Although I initially analysed results without the five cases still autocorrelated at a 48-hour interval, the pattern did not change when they were included for re-analysis. Consequently, it is reasonable to assume that a 2-day interval between locations can be considered independent unless sampling periodicity is extensive. Obtaining fixes at the same time each day may introduce a bias from possible 'homing' behaviors (White and Garrott 1990).

Because the t^2/r^2 index can indicate that locations may be independent in a small time interval and autocorrelated over a larger time frame, the researcher must decide if such a smaller time frame but with independent data is appropriate for the question asked or whether autocorrelation indices should be ignored. Also, if a time to independence is estimated, the time interval over which monitoring occurs must be sufficient for the estimated parameter to be valid. Various activities (*e.g.*, foraging, scent-marking) may require extended periods of time before they include the individual's effective home range (Garton et al. 1985, White and Garrott 1990). The time period required for an individual to traverse its entire home range likely varies with the individual and other factors such as prey density, habitat, or geography. If insufficient time is not given for an individual to traverse its home range, then estimates will not be representative of the true home range area. This 'time to traverse' the home range certainly differs among species (*e.g.*, Garton et al. 1985, Swihart et al. 1988) and depends on how one defines home range (Harris et al. 1990).

2. Autocorrelation

The effect of autocorrelation was not significant for paired comparisons with equal sample sizes. However, autocorrelated data do have the potential to influence home range estimates. In all cases presented here, an autocorrelated data set equivalent in number to the paired independent data set was sampled over fewer days than the data set comprising only independent locations. Consequently, a coyote could be sampled in areas where it was not present earlier. One should always be aware of possible autocorrelation and perhaps minimize it, but HM and MCP methods appear robust to autocorrelational effects when sample sizes are reasonably large.

That HM and MCP methods are sensitive to sample size and assume independence of locations has been extensively documented (*e.g.*, Swihart and Slade 1985a, Harris et al. 1990, White and Garrott 1990). Furthermore, simulation studies have shown that autocorrelated locations tend to underestimate the home range size (Swihart and Slade 1985a). This study argues against such a bias when sample sizes are equal because the 95% HM and the 95% MCP did not change in a predictable way with autocorrelated locations (Fig. 2-2). However, if the difference in time span between comparisons is large then autocorrelated locations most certainly will underestimate the home range (unless migrations or dispersal movements are a factor or both time intervals are so large that the difference is of no consequence). Therefore, I tried to minimize the confounding effect of time span differences for this analysis.

3. Harmonic Mean vs Minimum Convex Polygon Estimates

The HM and the MCP methods provided dissimilar estimates of home range sizes for the coyotes examined here. When several assumptions considered important to both (White and Garrott 1990) are violated, disagreement between the two estimators would be expected. However, large discrepancies in estimates even after 2 major assumptions have been met (independent locations and an equal number of locations for each estimator), support the hypothesis that the HM and MCP methods provide very different estimates of home range size. The 95% HM tended to be at least three times greater than the 95% MCP.

In my analysis, estimates from the two methods were correlated ($r = 0.779$) when home range size estimates were first compared with entire data sets, indicating that about 61% (r^2) of the variation in one method could be accounted for by the other. Using the correlation equation to relate one method to the other, however, is not recommended because much of the variability (39%) remains unaccounted for and the harmonic mean method has proven to be notoriously imprecise in computer simulations (Boulanger and White 1990) and may lead to significantly different values each time. Indeed, when data sets were manipulated to meet the assumption of independence of locations with equal numbers of locations, the correlation was poor (r = 0.586). Consequently, these data support Boulanger and White's (1990) prediction that home range estimators would not produce comparable results with complex field data.

Determining which estimator is most appropriate has been an ongoing effort. Simulation studies by Boulanger and White (1990) found that overall, the harmonic mean estimator was the least biased among five home range estimators (Fourier series, harmonic mean, minimum convex polygon, Koeppl ellipse, and the Jennrich-Turner ellipse) but also one of the least precise (large standard deviations) when tested with their four simulated data patterns. However, the authors maintain that the flexibility of the harmonic mean method allows it to fit irregularly-shaped home ranges. Nevertheless, they suggest caution whenever using this estimator for small sample sizes. With simulated data, the MCP method offers little, if any, advantage over the HM method. The MCP method appears unpredictably biased in terms of home range size and shape although its precision seems to improve as sample size increases (Boulanger and White 1990). Unfortunately, without knowing the true home range size, the significance of one factor over the other cannot be accurately determined from field data. Clearly, interpretations about each home range method are heavily influenced by the sample size of the location data set (Boulanger and White 1990).

The MCP method achieves a 95% home range size estimate by simply ignoring 5% of the outermost points. The 95% HM method considers all locations for a home range size estimate but calculates a 95% probability ellipse for the 95% contour level. Therefore, the potential exists for the HM method that a few (2-3) points occur far from the main area of activity and generate a misleading estimate of home range size. This apparently occurred in the five cases where I omitted 1-3 points that produced much larger home range sizes than all the others. Although the 95% MCP may reduce the influence of outliers by eliminating 5% of the peripheral fixes, this procedure is clearly subjective (White and Garrott 1990).

Not surprisingly, large sample sizes are desirable for home range estimators which is not likely to change. With large sample sizes, the HM and MCP methods appear robust to autocorrelation. For small sample sizes (*e.g.*, <30) over a short time interval (*e.g.*, 2 weeks), a HM estimate may not be possible. Although the MCP can enclose a small number of locations and thus provide an estimate under these restrictions, the researcher is always confronted with determining if these restrictions are representative for the estimated parameter. For home range studies, the pertinent question becomes did the individual have sufficient time available in which to traverse the effective home range (White and Garrott 1990)?

4. When To Use Home Range Size

At present, variation in home range sizes reported for coyotes is not understood which has precluded synthesis and generalization (Laundré and Keller 1984, Andelt 1987). Variation in data collection procedures, geography, and the idiosyncrasies associated with the present home range estimators have complicated the interpretation of the home range concept which will restrict it use to an index of activity. Home range estimation methods used today serve only to confound the biological meaning of the index. Some of the variance is certainly due to current analysis procedures as shown here. Part of the problem arises from the three dimensional nature (x,y,t) of relocation data while most home range techniques widely used today operate only in two dimensions (x,y), explicitly ignoring the time (t) component of location data. If home ranges are a suitable method to index animal activity and not an anthropogenic concept (*i.e.*, there is biological significance to home range size and shape) then more appropriate techniques are needed.

Currently, there is no home range estimator that makes no assumptions about shape that also incorporate the time dimension of location data (White and Garrott 1990). Until a method without such assumptions is introduced and tested, home range indices can only be considered as general approximations of activity area. Furthermore, unless biological significance for home range size and shape can be demonstrated for the animal of interest, reporting individual home ranges has little meaning (Sanderson 1966, Smith et al. 1981, Laundré and Keller 1984, White and Garrott 1990).

Home range size and shape, however, may retain some utility where crude measurements are still acceptable. Nevertheless, publishing home ranges by themselves should be discouraged, at least for coyotes. Calculating home range sizes when testing hypotheses within a study area is useful when an hypothesis predicts changes in the size of home range. Therefore, reporting home range size only becomes useful as an index of change when exploring some other ecological parameter. However, which home range method to implement must be considered as estimates of home range size can be influenced by method.

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Table 2-1. Minimum time interval required between consecutive locations of coyotes to achieve statistical independence based on Schoener's (1981) t^2/r^2 ratio. The index compares the mean squared distance between consecutive locations (t^2) to the mean squared distance of each observation from the centre of activity (r^2). Because the tested hypothesis is that locations are independent, an $\alpha = 0.25$ would reduce the probability of committing a type II error. Therefore, minimum times for independence are usually greater than those for $\alpha = 0.05$. Tests for independence of locations did not extend beyond 48 hours between consecutive locations.

COYOTE	MINIMUM TIME INTERVAL (hrs)			
	$\alpha = 0.05$		$\alpha = 0.25$	
	Hours	n	Hours	n
WINTER				
C04-w90	12	84	16	68
C04-w89	24	52	>24	52
C07	>48	21	>48	21
C08	12	61	24	46
C11	36	37	36	37
C17-w90	12	92	16	72
C17-w89	12	61	16	55
C20-w90	16	43	>24	37
C20-w89	>48	15	>48	15
C21	12	92	24	60
C22	12-16	71	16	71
C23	>48	34	>48	34
C31	20	60	>24	55
SUMMER				
C04	>48	42	>48	42
C17	32	46	32	46
C22	3	128	6	110
C22-seq	3	98	6	72
C31	>48	30	>48	30
C68	3	123	6	96
C68-seq	24	13	3	50

Table 2-2. Comparison of 95% harmonic mean and 95% minimum convex polygon home ranges estimates (km^2) for radio-collared coyotes in southwestern Manitoba, 1989-90. Harmonic means are reported with the original sample size and after removing the initially detected outliers (if applicable). The presence of autocorrelation in the original data set is given by the indices t^2/r^2 (1), psi (2), and gamma (3) when these values were statistically significant.

COYOTE	AUTO-CORRELATION INDEX	HARMONIC MEAN (n)		MINIMUM CONVEX POLYGON
		(with outliers)	(outliers removed)	
C04S90	1,2	13.2 (49)	13.2 (49)	9.0 (46)
C04W90	1,2	33.1 (121)	16.4 (118)	14.2 (115)
C04S89	1,2,3	25.0 (409)	23.2 * (346)	12.9 (388)
C04W89	1,2,3	38.7 (95)	28.0 (91)	22.8 (90)
C05ALL	none	53.3 (32)	32.2 (31)	19.7 (30)
C07W89	1,2,3	80.1 (72)	80.1 (72)	43.3 (68)
C08W89	1,2	38.5 (66)	38.5 (66)	22.3 (62)
C11W89	1,2,3	14.2 (96)	3.2 (82)	8.1 (91)
C17W90	1,2	29.8 (130)	4.5 (109)	12.0 (123)
C17S89	1,2,3	39.5 (184)	6.9 * (156)	15.1 (174)
C17W89	2	29.8 (72)	25.9 (69)	13.8 (68)
C19ALL	1,2,3	61.3 (86)	49.0 * (84)	38.0 (81)
C20W90	1,2,3	31.7 (81)	27.3 * (67)	7.0 (77)
C20W89	1,2,3	123.2 (41)	66.4 * (36)	44.7 (38)
C21W90	1,2	32.8 (141)	19.0 * (118)	11.5 (134)
C21S89	1,2,3	42.4 (157)	18.6 (153)	22.2 (149)
C22S90	1,2,3	23.4 (316)	0.5 (255)	7.8 (300)
C22W90	1	31.2 (152)	5.6 (123)	7.5 (144)
C22S89	none	12.5 (32)	12.5 (32)	5.9 (30)
C23W90	1,2,3	47.5 (130)	12.0 * (110)	15.9 (123)
C23S89	1,2,3	25.2 (114)	4.5 * (108)	3.9 (108)
C25W90	1,2	79.2 (30)	8.1 † (29)	5.4 (28)
C27W90	1,2	20.8 (128)	7.3 * (115)	5.5 (121)
C31S90	1,2	8.2 (83)	0.2 * (75)	3.0 (78)
C31W90	1,2,3	32.3 (138)	23.8 * (116)	17.5 (131)
C67ALL	none	14.6 (34)	15.3 * (30)	7.9 (32)
C68S90	1,2,3	28.2 (271)	10.1 * (221)	7.4 (257)

* additional outliers identified after initial outliers removed.
† no significant core area found.

Table 2-3. Relationship of the 95% harmonic mean and 95% minimum convex polygon (MCP) home range estimates (km^2) for radio-collared coyotes in southwestern Manitoba, 1989-90 using serially correlated and independent locations from the same season. Both autocorrelation indices t^2/r^2 and ψ (psi) needed to be significant before a data set was considered autocorrelated (see text). Although estimates are based on the same sample size (n) the 95% HM generates a probability ellipse based on all locations while the 95% MCP ignores 5% of these locations by design.

COYOTE	HARMONIC MEAN			MINIMUM CONVEX POLYGON		
	Independent	Autocorrelated	n	Independent	Autocorrelated	n
C04W90	25.2	29.1	55	11.3	14.7	52
C04S89 *	33.8	14.2	42	5.5	7.1	39
C04W89	32.4	31.8	30	16.0	17.2	28
C08W89	39.8	35.4	48	20.3	21.4	45
C11W89	11.1	14.7	37	4.9	6.2	35
C17W90	30.6	34.4	55	11.6	6.8	52
C17S89	48.1	47.5	46	6.2	5.6	43
C17W89	57.4	45.7	36	12.8	13.1	34
C20W90	33.1	105.5	36	4.1	7.9	34
C21W90	33.0	48.9	58	10.9	7.6	55
C21S89	28.1	25.3	50	14.3	14.4	47
C22S90	16.3	13.1	53	4.8	4.9	50
C22W90	30.9	19.1	62	6.0	2.2	58
C23W90 *	34.9	62.3	34	14.2	8.8	32
C27W90	14.4	21.3	57	5.3	4.7	54
C31S90 *	9.5	8.5	30	3.1	2.7	28
C31W90	19.2	30.1	41	6.9	7.4	38
C68S90	14.2	4.2	38	2.7	1.4	36

* Autocorrelation indices calculated for consecutive location up to 48 hours apart suggest no independence. In these cases, consecutive locations were considered independent after 48 hours and were included with the others after no change in pattern occurred in a separate analysis.

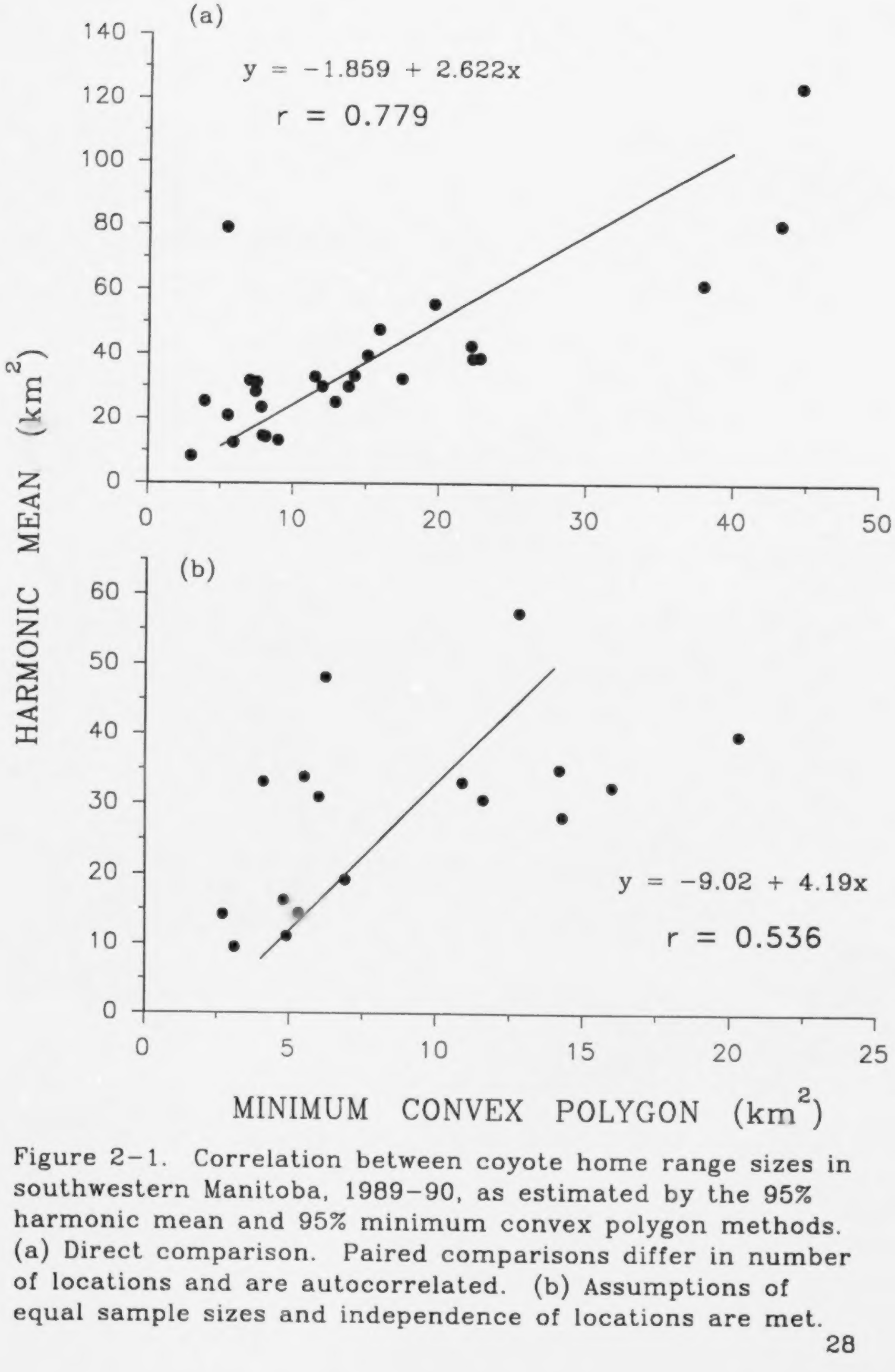

Figure 2–1. Correlation between coyote home range sizes in southwestern Manitoba, 1989–90, as estimated by the 95% harmonic mean and 95% minimum convex polygon methods. (a) Direct comparison. Paired comparisons differ in number of locations and are autocorrelated. (b) Assumptions of equal sample sizes and independence of locations are met.

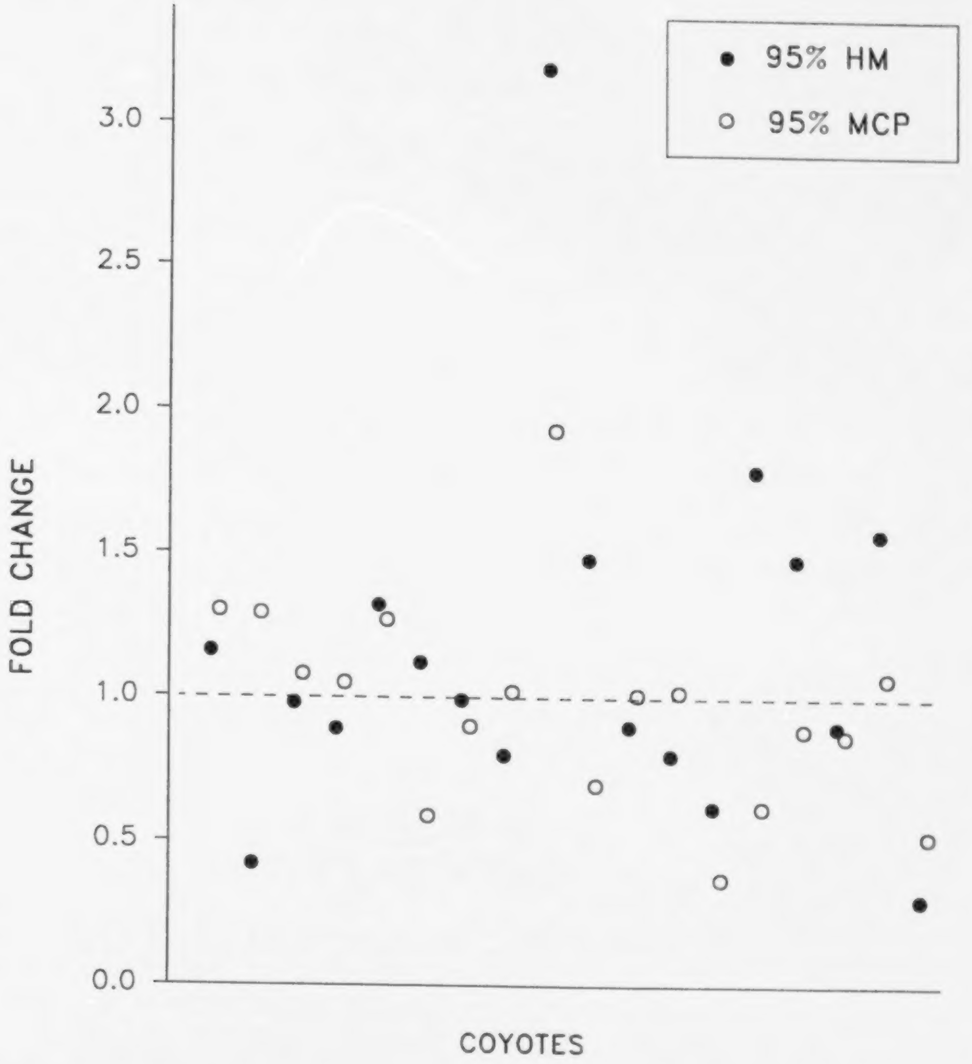

Figure 2-2. Effect of autocorrelation on coyote home range sizes (km^2) in southwestern Manitoba, 1989-90, as estimated by the 95% harmonic mean (HM) and 95% minimum convex polygon (MCP) methods. Fold change is determined from home range sizes calculated with autocorrelated location divided estimates based only on independent locations. Sample sizes equal within each paired compaison. A fold change of 1.0 represents no change.

CHAPTER 3

SUMMER ACTIVITY PATTERNS OF DENNING COYOTES IN SOUTHWESTERN MANITOBA

INTRODUCTION

Coyotes are strictly monogamous mammals and exhibit biparental care of their young (Kleiman 1977, Voigt and Berg 1987, Moehlman 1989). Involving the male of the pair in pup-rearing may allow larger litter sizes and greater pup survival than when only the female raises her litter (Moehlman 1989). For silverbacked jackals (*Canis mesomelas*) , the female cannot raise a litter on her own without substantial male investment (Moehlman 1989). Consequently, a strong incentive would exist for the male to assume an active role in providing for his offspring. While the female would nurse her pups, the male (and possibly other related adults) would contribute by provisioning the female and her litter (van Wormer 1964, Gier 1975, Moehlman 1979, 1981, 1989). As pups are weaned, the breeding female may increase her foraging effort for both herself and her pups unless pup vulnerability requires their protection from outside aggression (*e.g.*, Camenzind 1978). The male may share pup protection duties with the female or he may modify his foraging effort to provide nutrition for the growing pups. However, the role of the male in pup-rearing may be more comprehensive if intangible benefits such as pup protection through male territory defense are significant (Clutton-Brock 1991).

Our knowledge of den use and spatial interactions of mated coyotes is fragmentary (Andelt et al. 1979). Contributing to this dearth of information is the elusive nature of coyotes and that few studies (Smith et al. 1981, Messier and Barrette 1982, Harrison 1983, Andelt 1985, Bekoff and Wells 1982,1986) have intensively monitored individual coyotes in an attempt to increase our understanding of pup-rearing behavior. Although Andelt (1985) monitored coyotes throughout the pup-rearing season, activity patterns among the nursing and post-nursing periods were not compared. Consequently, possible changes in parental roles were not determined, but he did document the interaction of denning adults and associate adults ('helpers') with pups for the nursing period. Andelt (1985) found no reduction in the amount of time that pups were left unattended by parents when associate adults were included in the group. Bekoff and Wells (1986) also reported no difference in the proportion of time a denning female allocated to den attendance when helpers were present. Furthermore, no difference in time spent around the den occurred between the dominant male and female pair in a pack of coyotes (Bekoff and Wells 1986). The female of a resident pair may spend a greater proportion of time around dens than her mate (Bekoff and Wells 1986) or differences between parents are not statistically significant (Harrison and Gilbert 1985). Whether the male changes his role during pup-rearing remains unclear (Laundré and Keller 1984).

Harrison (1983) and Harrison and Gilbert (1985) suggested that adult coyotes increase their movements and expand their home ranges during weaning of pups. However, average distances that radio-collared adults were located from den or rendezvous sites (Harrison and Gilbert 1985) did not change between nursing and weaning, suggesting attendance of pups may remain a frequent activity even after pups are weaned. Caturano (1983) and Witham (1977) reported that females occupy smaller home ranges during May through July relative to other times of the year. Laundré (1979) demonstrated that females coyotes use smaller areas during pup-rearing than in other seasons but he did not investigate potential changes within the pup-rearing season. Bowen (1978) also reported no difference in home range area during pup-rearing relative to composite home ranges although he only considered solar seasons rather than reproductive seasons for coyotes (*e.g.*, Laundré and Keller 1984). Consequently, additional effort is needed to investigate the role of the parents during pup-rearing.

In this analysis, I addressed the movement patterns of denning coyotes during the pup-rearing period in summer. I used radio-locations of denning adult coyotes to monitor the time adult coyotes spent at the den site with pups. I documented times, durations, and distances of excursions from the den site of adult males and females to examine if these activities differed between the sexes and changed throughout the summer based on the development of pups.

METHODS

1. STUDY AREA

The study area encompassed a 150 km^2 region consisting of part of the southern boundary of Riding Mountain National Park (RMNP) in southwestern Manitoba (50° 40' lat., 100° 10' long.), Canada and adjacent lands outside the park. Within RMNP, dominant cover comprises the boreal mixed-wood forest, although the proportion of aspen (*Populus* spp.) to spruce (*Picea* spp.) is greater in the study area than in other areas of the park. Aspen parkland dominated by agriculture completely surrounds RMNP such that the park may act as an ecological island (2976 km^2) of trees (see Appendix 1 for a detailed description of the study area). Radio-collared coyotes commonly traveled in and out of the park. A network of roadways outside RMNP allowed vehicle access for monitoring coyotes no further than 1.6 to 3.2 km away. The lower density of roads and vehicle restrictions inside RMNP, however, reduced my ability to get closer to radio-collared coyotes than when located outside the park.

2. CAPTURE, MARKING, AND MONITORING OF COYOTES

I trapped coyotes with padded leghold traps, and eartagged and fitted each with a radio-collar (see Appendix 2 for capture data). Trapping was not permitted inside park boundaries but occurred on adjacent agricultural areas. Captured individuals were classified by sex and age. I estimated age classes by body size and dentition (Appendix 2). Age classes followed Andelt (1985) and Gese et al. (1988).

I delimited home ranges and identified suspected den and rendezvous sites (Harrison and Gilbert 1985) of coyotes by monitoring yearlings and adults by radio-tracking daily. Adult coyotes with den sites located in areas that facilitated frequent daily monitoring by ground vehicle were used as focal individuals to investigate natal den attendance from May to August, 1989 and 1990. I used sequential sampling (Laundré and Keller 1984) to monitor the hourly movements of focal individuals throughout the 24-hr day for 2-week periods in June and July. At other times, coyotes were usually monitored once daily either during day or night. Sequential sampling periods comprised four hourly radio-locations of which three or four sampling periods were monitored in any one 24-hr period. Time slots began at 03:00, 07:00, 11:00, 15:00, 19:00, and 23:00. Consequently, four locations were obtained for the coyote(s) monitored during each time interval. I monitored 8, 6, 6, 4, 8, and 6 times from each of the six 4-hr monitoring periods in June, respectively and 4, 10, 4, 4, 10, 4 times in July, respectively.

Locations were estimated by triangulation from bearings obtained by a hand-held antenna from a ground vehicle. Normally three bearings were taken for each location estimate although locations based on two or four bearings were also used. The ad hoc method (Nams and Boutin 1991) was used to initially reject locations considered too imprecise. The error triangle technique (Nams and Boutin 1991) formed the basis of estimating an individual's location although the probability of the estimate containing the true location could not be determined (Nams and Boutin 1991). However, reference transmitters at known locations were used to estimate the accuracy and precision of the triangulation procedure using the maximum likelihood estimator (Lenth 1981) provided in the LOCATE II program (Nams 1990). Based on these reference transmitters, bearing error was estimated at ±2.0°. I used program HOME

RANGE (Ackerman et al. 1990) to estimate home range size. Visual observations were incorporated into the analysis whenever they occurred, primarily as indicators of group associations.

I identified three biological seasons for coyotes in summer based on pup development in the domestic dog (Sessions 1972). Observations by Snow (1967) and Gier (1975) suggest similar development in captive coyotes. I used May as the 4-week nursing period because Sessions (1972) identified the first four weeks of a pup's life as a time when it is completely dependent upon its mother and because coyotes have whelped by the first week in May (pers. observation). I divided the post nursing period into June (Part A) and July and August (Part B). Post-nursing period A reflects the 5th-7th week (inclusive) where the pup becomes more aware of its surroundings and socializes with the litter (Sessions 1972). From the 8th week on, the pup is receptive to learning, is more mobile, and may be left unattended for longer periods. Consequently, post-nursing period B began when pups were about eight weeks old and continued until monitoring ended on 31 August.

3. LOCATION OF DEN SITES

I investigated areas where radio-locations of individuals were concentrated, especially during the afternoon, for potential den sites. Initial den searches were done before leaves flushed, normally by mid-May. Ideally, I searched for dens when the individual, especially if female, was away from the den. I only searched for dens when the female coyote was thought to be inside if previous attempts to locate the den were unsuccessful. Unsuccessful attempts were with den sites located inside RMNP rather than in woodlots outside the park. Occasionally I delayed a search for a den site until later in the summer to avoid possible abandonment of the den from human disturbance. I also monitored den sites that were active in previous years.

4. DEN ATTENDANCE

4.1 Determining the Active Den Site

No standardized criteria have been developed to determine den site attendance by radio-locations. Because triangulation of radio-collared individuals only provides an estimate of an individual's location, the error associated with that estimate may place an individual at given location although it may be only nearby. However, individuals may also venture a short distance (*e.g.*, 100m) from the den site for whatever reason but still may be considered 'at the den' (Andelt 1985, Harrison and Gilbert 1985).

Rather than arbitrarily deciding on an effective area for a den or rendezvous site (collectively called 'home site'), I tried using the radio-locations of denning coyotes where their home sites were known throughout the summer to define the active home site (Harrison and Gilbert 1985). Initially, I used the method of Harrison (1983) where increases in home site radius (by 100m increments) are examined for their influence on the proportion of locations considered at the home site. A change in the percent cumulative frequency of locations considered at the home site as the site radius increased would determine if home site attendance could extend beyond the physical den or rendezvous site itself. I recalculated frequencies at the den at the individual level. This time I increased the radius from the den as concentric circles each having the same area beginning at 200m. Consequently, I incremented the radius from the den by a factor of 1.41 ($\sqrt{2}$) because the equation of a circle is πr^2. I expected an abrupt change in the number of locations within concentric areas as radius from the den increased. I defined the limits of being at the den with respect to this point. When no den site radius could be determined in this manner, I followed Harrison and Gilbert (1985) and considered locations within 300m from the physical den site as being at the den.

4.2 Movement Patterns

I used locations of radio-collared adult coyotes having den or rendezvous sites to test for changes in home range areas during summer, determine the time spent at the home site, and estimate the duration of their excursions from this site. Home range size was estimated by the 100% minimum convex polygon method (Mohr 1947, White and Garrott 1990) because I tried to delimit the entire area used by the coyotes during the specified time frame. I compared area used in summer with composite home ranges that included locations from more than one season. Home range size estimates were based on consecutive locations at least three hours apart and again when at least 12 hours apart in order to reduce bias from autocorrelated locations (Swihart and Slade 1985). Three and 12 hours separating consecutive locations were considered acceptable because of the apparent robustness of the minimum convex polygon method to autocorrelated locations if the number of locations is relatively large and does not occur in a small time frame (see Chapter 2).

I used the binomial distribution to put confidence limits on the probability of males and females being at the home site over a 24-hour period and throughout the summer. I monitored a mated pair of radio-collared coyotes in June and July, 1990 to determine parental roles within a group during pup-rearing. I grouped daily locations into six 4-hr time intervals beginning at midnight. I used sequential monitoring to approximate the duration of coyote excursions from the home site. Because time slots assigned for monitoring were limited and only four hours long, many excursions were joined in progress and/or not followed to completion. Although monitoring often occurred over adjacent time slots, extended excursions from the home site could not always be documented, consequently, excursion durations would be biased low. When the onset or completion of an excursion by a monitored coyote was unknown, I added 0.5 hr to either the time monitoring began or after monitoring had ended, as appropriate. I used 0.5 hr because this was one-half of the average time between consecutive radio-locations. I also estimated activity by calculating movement rates of coyotes based on the straight line distance between two locations approximately one hour apart (range 0.75 to 1.25 hours). Although I added carcasses as food supplements to an experimental group of coyotes to compare with a control group where no food was added, carcasses either spoiled or were consumed by other scavengers. Coyotes seldom used the site as a food source (see Appendix 4 for details) such that no significance was attributed to the effort and consequently the food addition was ignored.

For statistical analysis of differences in frequency data, I used the *G* test with the Williams correction because of its ease of use and additivity property that would allow multi-year comparisons (Sokal and Rohlf 1981). To examine for differences in activity during pup-rearing stages, I used a 2-way factorial randomized block design ANOVA with sex and time period as the main effects. I used a pairwise *t*-test to look for differences in time period within an individual. I considered differences statistically significant at the $\alpha \leq 0.05$ level.

RESULTS

1. COYOTES WITH DENS

Three adult female coyotes and two adult males associated with den sites were monitored in either 1989 or 1990 (Table 3-1). One mated pair (C68 and C22) was monitored sequentially in 1990. Known home sites (dens and rendezvous sites) used for pup-rearing by these coyotes varied from one to seven in any one year (Table 3-1). When monitoring continued throughout the summer, coyotes occupied at least two home sites. The occurrence of only one den site for female coyotes C04, C27, and C68 in 1991 reflect the brief 2-week monitoring period in May. Den sites were more difficult to locate when only the male was radio-collared, possibly because they may not always be inside the den. The use of seven home sites by coyote C04 and five home sites by coyote C17 in 1989 were likely due to disturbances resulting from this study (Table 3-1). Coyote C04 terminated her pup rearing activities in May 1990 by completely abandoning her den and her six pups, also as a result of human disturbance (detailed in Section 5.2).

2. HOME RANGES

Composite home ranges of coyotes C04, C17, C68, C22, and C31 were 20.1, 19.9, 7.4, 10.4, and 15.7 km^2 respectively. Overall, average decrease in home range size from composites to the weaning period (May and June) was 42% (S.E. = 7.3%). Females (C04, C17, and C68) averaged a 47% decrease (S.E.= 1.54) while the two males ($\overline{X}$= 32.8%, S.E. = 20.10) showed a significantly lower decrease than females ($t_{(3)} = 3.887$, $p < 0.05$). No significant differences in home range size occurred within the different pup-rearing periods ($F_{2,7} = 3.40$, $p = 0.093$) for adult coyotes with dens whether home range sizes were measured using consecutive locations ≥3 or ≥12 hours apart (Table 3-2). Whether core activity areas increased from May to July/August was not clear because core areas were not identified by the harmonic mean method for two coyotes (Table 3-2). Home range sizes estimated with consecutive locations at least three hours apart during pup-rearing were different between the sexes ($F_{1,10} = 6.52$, $p = 0.029$). Time period had no effect ($F_{2,12} = 2.12$, $p = 0.171$). When consecutive locations at least 12 hours apart were used to estimate home range sizes, sample sizes were reduced and the difference between the sexes disappeared ($F_{1,10} = 2.44$, $p = 0.137$).

3. PROXIMITY TO THE HOME SITE

The proportion of radio-locations from adult coyotes considered 'at the den' for a 6-week period beginning in May did not show a marked asymptote as radius from the actual home site increased from 100 to 1000m (Fig. 3-1). However, percent cumulative frequency curves from the increasing radius from the den site (Fig. 3-1) were different for the two male and three female coyotes (2x10 contingency test, $G_{(9)}$= 46.096, $p < 0.001$). Although sampling times during the day (in eight 3-hr intervals) for these coyotes were significantly different from random ($G_{(7)} = 46.871$,

$p < 0.001$), all eight time intervals were thought to have been adequately represented, with the lowest sampling frequency at 21 times for the 0300-0600 hour interval.

The number of locations in concentric circles radiating from the den site differed for males and females (Figs. 3-2 and 3-3). For females, the frequency of locations differed significantly among increasing radii from the den ($G_{(16)} = 69.415$, $p < 0.05$). However, the subset of radii beyond 200m was not significantly different for the three females ($G_{(16)} = 23.646$, $p = 0.098$). However, because the number of locations between 200m and 283m were above 10% for coyotes C04 and C17, and 20% for coyote C68, I decided to consider locations ≤300m from the den or rendezvous site as being at the site. Although the frequency of locations of female coyotes C04 and C17 considered at the den were not different from each other ($G_{(16)} = 12.782$, $p = 0.68$), I was unsure how coyote C68 corresponded with the other two females because of the smaller number of locations for C68 (Fig. 3-2). No significant difference in locations occurred for males for any one radius ($G_{(8)} = 15.507$, $p = 0.93$). Consequently, I also considered locations of males ≤300m from the den or rendezvous site as at the site.

There is some suggestion that males and females differ in their probability of being at the den during nursing and early post-nursing periods but any distinction disappears by July and August (Fig. 3-4). Binomial probabilities (± S.E.) for adult female coyotes averaged 0.606 (± 0.069), 0.612 (± 0.044), and 0.394 (± 0.027) over the 24-hour day during May, June, and July/August respectively. Similarly, average probabilities (± S.E.) for males were 0.410 (± 0.052), 0.397 (± 0.057), 0.394 (±0.027). However, when a mated pair was monitored sequentially for two weeks in June and in July, males showed virtually no difference from females (Fig. 3-5).

4. EXCURSIONS FROM THE HOME SITE

Movement patterns of the mated pair during sequential monitoring period in June and July indicated large variation in movement rates throughout a 24-hr period (Fig. 3-6) confirming that coyotes may be active at any time of the day. Activity in June was lowest from mid-afternoon to early evening prior to sunset. Both the male and the female behaved similarly for most of the day except during mid- to late morning where the male showed greater variation than the female in his movements (Fig. 3-6). Movement rates in July for both members of the pair were more erratic than in June and indicated more activity in mid- to late afternoon (Fig. 3-6). Variation in movement for both the male and female was greatest in July about an hour after midnight, possibly indicating that males and females alternated in attendance at the den. However, only four sampling intervals included the midnight and 01:00 period for July, and all three possibilities of parents in relation to the den occurred (both parents present, one parent only, and no parents present).

In May, coyote C22 was not at the den for 41% of 17 locations. (No estimate is available for the female, C68, because she was not radio-collared until 28 May). During the first post-nursing period (June), female coyote C68 was absent from the den 57% of the 165 locations taken during sequential monitoring. Similarly, mate C22 was located away from the den for 63% of these 165 locations. In the second post-nursing period (July and August), absence from the den was 63% and 73% for female and male respectively for 153 locations. Only in 21% and 12% of the locations in June and July/August respectively, were both parents present at the den during monitoring. For over half (20 of 35) of these occurrences, both parents were at the den between the 16:00 to midnight period. Pups were left unattended for 42% of the time in June and increased slightly to 48% for July (Fig. 3-7). The increase in July was manifested in greater movements of parents away from the home site at crepuscular times (Fig. 3-7). Both parents were away from the home site more often between midnight and 08:00 h in June (Fig. 3-6). In July, absence of both parents from the home site increased from June between 16:00-20:00h.

I believed that C68 and C22 were without any adult associates helping at the den. In winter, both aerial and ground monitoring suggested that no other coyotes were associated with the mated pair. In summer, when either C68 or C22 was present at the den site, only single vocalizations occurred at the den in response to a preceeding single vocalization were I had just located the mate. I expected that other coyotes would have joined in the vocalizations if they were present, however, I never heard more than one coyote whenever I had located either C68 or C22. From radio-locations and occasional ground sightings in summer, the mated pair seldom foraged together.

The average distance traveled by coyotes on excursions increased from 2.4 km in June to 3.6 km in July and August (Table 3-3). Maximum distances may exceed eight km, however. The amount of time an excursion from the home site ensues averaged about three hours in June but was an hour longer in the July and August period (Table 3-3). No significant differences were detected between coyotes or the June and July sequential sampling periods. However, estimates are biased low because monitoring periods were not always able to incorporate the entire trip from the home site and its return. Consequently, longer excursion durations would be under-represented. Data were insufficient to compare males and females and to precisely determine the number of trips taken by adults in a day. Consequently, increased effort on behalf of the parents once pups were weaned could not be demonstrated in this way.

5. DISTURBANCE

5.1 Den Site Relocation

Five adult female coyotes known to have dens (C04, C17, C27, C31, and C68) relocated to another den site from their initial natal den at least once in any one year

(Table 3-1). Coyote C04 relocated to new sites six times in 1990 (Table 3-1). Seven den relocations I attributed to my disturbance once I had discovered the den. When a den was first discovered, I checked the entrance to listen for sounds of pups, after which I promptly left the area. However, it is not clear if my presence alone precipitated the subsequent den site relocation because none of the seven instances received only this minimal level of disturbance. Five relocation occurrences had repeated visits by humans (a result of observation attempts), whereas three den sites were located when the female was present inside the den. In one of these cases (C17 in 1989), the female left the den just as I approached the site.

5.2 Pup Abandonment

Female coyote C04 abandoned her den with the pups inside in 1990 (Table 3-1) after I had made repeated visits to the den area in hopes of recapturing her to replace her weak radio-collar and obtain a blood sample for genetic analysis. Based on relocations by C04 the previous year, I had hoped to recapture her as she would relocate her den after my intentional disturbance. Unfortunately, she unexpectedly abandoned the den on 11 May. On 14 May I dug out six pups from C04's den, all of which I initially thought were dead. However, I was able to revive two of them. I put the two pups back into the den the following night hoping that the mother would reclaim them. However, this did not occur and one pup died later that day after I retrieved them from the den the second time. The one remaining pup (female) was successfully revived again and raised in captivity.

DISCUSSION

1. DEN AND RENDEZVOUS SITES

The transition from den to rendezvous sites for coyotes reportedly occurs when pups are 8-10 weeks old (Harrison and Gilbert 1985). However, most studies of coyotes have not distinguished between den and rendezvous sites, if the latter do indeed occur. If coyotes use rendezvous sites as described for wolves (Murie 1944, Joslin 1967), then the transition from den to rendezvous sites may mark the change in parental care and foraging behavior as pups attain a given level of development. Rendezvous sites of wolves comprise a system of trails, beds, and activity areas where the pups remain most of the time while adults are often away, presumably hunting (Joslin 1967). Nursing dens used by coyotes are consistent with the altricial nature of newborn pups and the protection they require. Nevertheless, coyote dens are variable likely vary with available habitat and latitude. Den sites of coyotes may be a burrow in the ground (*e.g.*, Althoff 1980) or under buildings or tunnels in brush piles, hedges, thickets (*e.g.*, Hallett et al. 1985) or even in blocked road culverts (M. Gibeau, Banff National Park, pers. commun.). However, shallow depressions at the bases of trees have also been reported as pup-rearing 'den' sites for coyotes in Kansas (Gier 1968) and Maine (Hilton 1978, Harrison and Gilbert 1985).

In this study, no den (burrow) was found at suspected rendezvous sites (when these sites were checked when they were no longer in use). By this time pups may be less vulnerable to adverse weather conditions and are less susceptible to some predators such as owls (*e.g., Stryx* spp.). As a result, pup protection by parents may be reduced and their foraging activity increased. Based on radio-locations, the timing for the move to rendezvous sites from dens in the RMNP area was imprecise and seemed to occur between mid-June to mid-July or when the coyote pups were about 7.5-11 weeks old (Table 3-1). Although use of a rendezvous site may extend until mid-October (Harrison 1983), I could not determine their extent of use here because monitoring did not occur in the fall. In one family group where I had the adult female, three of her pups, and a suspected helper radio-collared, the first time that these pups traveled with an adult occurred on 30 August.

2. TIME SPENT AT THE HOME SITE

How much time adult coyotes spend at a den or rendezvous site depends on the effective area of use around the site. Andelt et al. (1979) considered coyotes at a den when locations of radio-collared coyotes were situated within 200m of the den site. Harrison (1983), however, observed adult coyotes resting >200m from the den and found that changes in den site radii and the percentage of locations considered at the den were less sensitive between 400-600m. Consequently, Harrison (1983) considered a 500m radius from the den as the effective den site but later used 300m (Harrison and Gilbert 1985). I conservatively considered locations of individuals ≤300m from the precise location of a home site as being at the site. I based this on the number of locations in concentric rings of equal area from the den site. However, locations ≤200m may have also been suitable. Males showed a more linear relationship for percent cumulative frequency and home site radius (Fig. 3-1) and no difference in the number of locations in concentric rings from the den site (Fig. 3-3). Therefore, they may simply stay at the actual site and leave when necessary without 'loitering' nearby. The female, on the other hand, may remain near the den when temporarily exiting the burrow, possibly to defecate or obtain water. When the pups outgrow the den and venture outside, the adult female would rest nearby. If telemetry error is small and constant (*e.g.*, ≤1 ha), frequent sequential monitoring would detect an excursion from the home site at one point and a return to the site for the next location. Alternatively, telemetry error and the few coyotes that were monitored here may contribute to spurious interpretations. However, active den sites seem devoid of prey remains and adult scats (Hallett 1977, Harrison and Gilbert 1985, pers. observ.) and would be consistent with the 'quick trip' hypothesis.

During pup-rearing, adult coyotes may be active at any time of the day. The amount of time spent at a home site, however, changes with the development of the pups. The degree of change seems greatest with the adult female because of the lactational demands of her pups. However, even after weaning, females may still frequent the den until pups are at least nine weeks old (Harrison and Gilbert 1985). Denning females spend over half their time at a den site in May, which changes little in June. Den attendance in July and August declines but still remains high (averages about 40%). Any one stay at the home site averages about 2.5-3.0 hours through the early summer period. Pup protection likely influences this behavior (Harrison and Gilbert 1985) as coyotes have been known to kill pups from a different litter when the parents were away from the den (Camenzind 1978). Denning adult males are away more often than females from the den during pup-rearing. Before pups are weaned, the male hunts for food for both parents (Gier 1975), and as pups grow and demand more food, the male must continue his effort, along with the female and any 'helpers' (Bekoff and Wells 1986, Moehlman 1989) that may be present. Consequently, canids that make a larger prepartum investment by producing larger litters of relatively less developed neonates require substantial male investment in the rearing of young (Moehlman 1989). Therefore, the male parent is an integral part of pup-rearing in coyotes and successful parenting (increased pup survival) likely requires both parents (Gier 1975, Harrison and Gilbert 1985, Moehlman 1989).

3. EXCURSIONS

Based on hourly movement rates, coyote activity in summer is best described as nocturnal and crespuscular. This increase in activity from sunset to sunrise versus other times has been widely documented for coyotes (see Gipson and Sealander 1972, Andelt 1985, Holzman et al. 1992). In general, the extent of nocturnal activity has been attributed to the level of human disturbance and exploitation (Andelt 1985, Harrison and Gilbert 1985). However, daytime activity does increase during the breeding (January and February) season and during pup-rearing (Andelt 1985). In the RMNP area (51° latitude), daytime activity did appear to increase from June to July although only one pair of denning coyotes could be monitored intensively (Figs. 3-4, 3-5). High daily temperatures may contribute to the reduced activity as suggested by movement rates reported here. Although movement rates for coyote C68 were among the lowest in early afternoon in July, movement rates rose significantly by 17:00 hours (Fig. 3-5) although average den attendance probabilities showed little change between these time intervals (Fig. 3-4).

Nocturnal animals need not always be resting at specific times during daylight periods and some variability during high temperatures is still expected because dehydration would require periodic drinking for adults and escorted pups. Andelt (1985) did not dispute the potential influence of higher temperatures on daytime activity, however, he did not see a reduction in daytime activity that one would expect during other periods of the year when temperatures were lower. Consequently, other factors such as territorial behavior (*e.g.*, Camenzind 1978) may also contribute to increases in daytime activity at other times (Andelt 1985).

Distances covered during excursions of monitored coyotes varied from near zero to over 10 km. Maximum distances did not change from June to the July/August period although averages were higher in the latter. Because the variability of movements was also greater in July/August, it is unclear if adults had to travel greater distances (and for longer periods of time) as pups developed. No change in distances of time traveled would be consistent with the lack of significant change in home range sizes observed for a given summer period. It is expected that composite home range areas should be larger than areas in summer because size and shape of home ranges are dynamic variables (Huxley 1934, Bekoff and Wells 1986) and greater periods of time can influence the nature of available resources (Bekoff et al. 1984).

Harrison and Gilbert (1985) argued that changes in movement behavior of adult coyotes suggest adults hunt more selectively for large prey items once their pups are weaned. Although this may be true, measuring movement behavior from distances of locations from dens is suspect if dens are relocated, as was the case for Harrison and Gilbert (1985). Coyotes relocated their den sites in the RMNP area several times

(Table 3-1), consequently calculating distances to dens would be inconclusive because potential differences in prey densities within the coyote home range would confound any changes. Also, movements must not be estimated from independent locations based on large time intervals (*e.g.*, 24 hrs) because of their unpredicable relationship between these perceived movements and actual movements within the home range (Laundré et al. 1987).

4. DISTURBANCE

Coyotes commonly abandon a den site for another (Bekoff 1982). Any disturbance of the den area will likely result in relocation although other factors may be important (Dobie 1949, Gier 1968, Bekoff 1982). A den site that is visited while the female remains inside is presumably a more serious threat than when she is not. In one instance when I searched for the den of a radio-collared female, she suddenly left from inside her den as I approached. Later that night she relocated to another den about one km away. Den relocations by other coyotes did not occur immediately after the den was found when a search was conducted if the radio-collared female was not at the den. However, subsequent visits after a den's discovery likely initiated a site relocation. Consequently, if a search for a den is necessary, such a disturbance should not occur while the female remains inside (if a relocation is undesirable). Sometimes this situation is unavoidable because females seem to be at the den most of the daylight period in May. Therefore, locating a den is best accomplished with the female radio-collared to ascertain a precise search area and confirm her absence in the search area. Den searches are more difficult with only the male radio-collared because males seem to be spend less time at the den and are not a reliable indicator of female presence at the site.

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Table 3-1. Use of confirmed and suspected (?) den sites (D) and rendezvous areas (R) of adult radio-collared coyotes in the Riding Mountain National Park area, Manitoba, from May to August 1989 and 1990 but only in May for 1991. Only coyote C31 is male. Locations are reported in civilian UTM co-ordinates.

COYOTE	HOME SITE LOCATION	TIME OF USE	COMMENTS
C04	418250 5612500 D	≤03 May → ~08 May 1989	human disturbance
	418100 5612300 D	~08 May → ~18 May 1989	human disturbance
	418400 5611500 D?	~18 May → 27 May 1989	
	419100 5612100 D?	27 May → 02 June 1989	
	419300 5612600 D?	02 June → 01 July 1989	
	418000 5611200 D?	01 July → 15 July 1989	
	418300 5610900 R?	15 July → ≥29 Aug. 1989	
	418700 5613900 D	≤04 May → 13 May 1990	abandoned pups
	420750 5613050 D	≤05 May → unknown 1991	
C17 †	409550 5614750 D	≤05 May → 11 May 1989	human disturbance
	408600 5615200 D	11 May → ~26 May 1989	human disturbance
	408100 5615200 D?	~26 May → ~08 June 1989	
	407400 5616500 D?	~08 June → ≤17 July 1989	
	407300 5614600 R?	~17 July → ≥30 Aug. 1989	
	410500 5616200 D	≤10 May → ~18 May 1990	human disturbance?
	408000 5613800 D?	≤07 June → ~14 June 1990	
	unknown	≥15 June → ≥30 Aug. 1990	
C27	421700 5621200 D	≤09 May → 1-5 June 1990	human disturbance
	unknown	1-5 June → 30 Aug. 1990	
	422500 5618400 D	≤17 May → unknown 1991	
C31	412200 5618450 D	≤04 May → ~05 June 1990	
	412250 5617750 D	~05 June → ~21 June 1990	
	413000 5617800 R?	~21 June → ≥30 Aug. 1990	
C68 ‡	416150 5615000 D	≤24 May → 17 June 1990	den located in 1991
	415700 5615300 R?	17 June → 30 Aug. 1990	
	415400 5616550 D	≤05 May → unknown 1991	

† with yearling female coyote C21 in 1989.

‡ associated with adult male coyote C22 during summer 1990 but died during winter 1990/91 after regular monitoring had ended.

Table 3-2. Home range changes of adult radio-collared coyotes in southwestern Manitoba, 1989 and 1990, during summer pup-rearing periods based on the development of pups. Home ranges were estimated by the 100% minimum convex polygon (MCP) method. Core areas were calculated by the harmonic mean method when the number of locations permitted. Coyotes C68 and C22 were a mated pair when monitored in 1990.

COYOTE	TIME SPAN[1]	MAY[2]			JUNE			JULY/AUGUST		
		MCP	Core	n	MCP	Core	n	MCP	Core	n
C04 ♀	3	8.5	4.3	73	9.8	1.2	80	12.0	6.7	63
	12	3.6	4.7	32	11.5	11.2	40	8.8	1.7	36
C17 ♀	3	3.7	1.9	62	14.0	12.7	38	9.6	3.8	41
	12	1.8	0.4	31	9.3	13.8	27	7.0	3.4	29
C68 ♀	3	-	-	-	6.7	0.1	56	4.9	-	50
	12	-	-	-	2.3	-	31	4.7	-	29
C22 ♂	3	2.7	0.6	17	6.4	-	55	8.3	-	48
	12	2.7	0.4	15	4.8	0.1	31	4.4	1.4	28
C31 ♂	3	0.8	-	18	1.6	-	34	6.8	0.4	36
	12	0.8	1.2	16	1.3	-	25	6.4	0.1	31

[1] Minimum time interval (hours) required between consecutive locations.

[2] Time periods based on pup development in the domestic dog (Sessions 1972).

Table 3-3. Average estimated distances (km) traveled (± 1 S.E.) by adult radio-collared coyotes in excursions to and from den or rendezvous sites, southwestern Manitoba, 1989 and 1990. Estimates are based on hourly locations obtained for 12-16 hours/day for 2 weeks in June and in July. Monthly time intervals represent pup-nursing periods based on the development of pups (see text).

COYOTE	JUNE			JULY		
	Distance	Time Span (h)	n	Distance	Time Span (h)	n
C04 ♀	2.8 ± 0.41	2.6 ± 0.20	21	4.0 ± 0.81	4.2 ± 0.63	17
C17 ♀	2.1 ± 0.49	2.7 ± 0.26	4	5.4 ± 1.36	4.8 ± 0.94	7
C22 ♂	2.8 ± 0.59	3.6 ± 0.38	17	2.9 ± 0.41	3.8 ± 0.46	18
C68 ♀	2.0 ± 0.37	3.2 ± 0.32	19	2.1 ± 0.24	3.3 ± 0.27	24

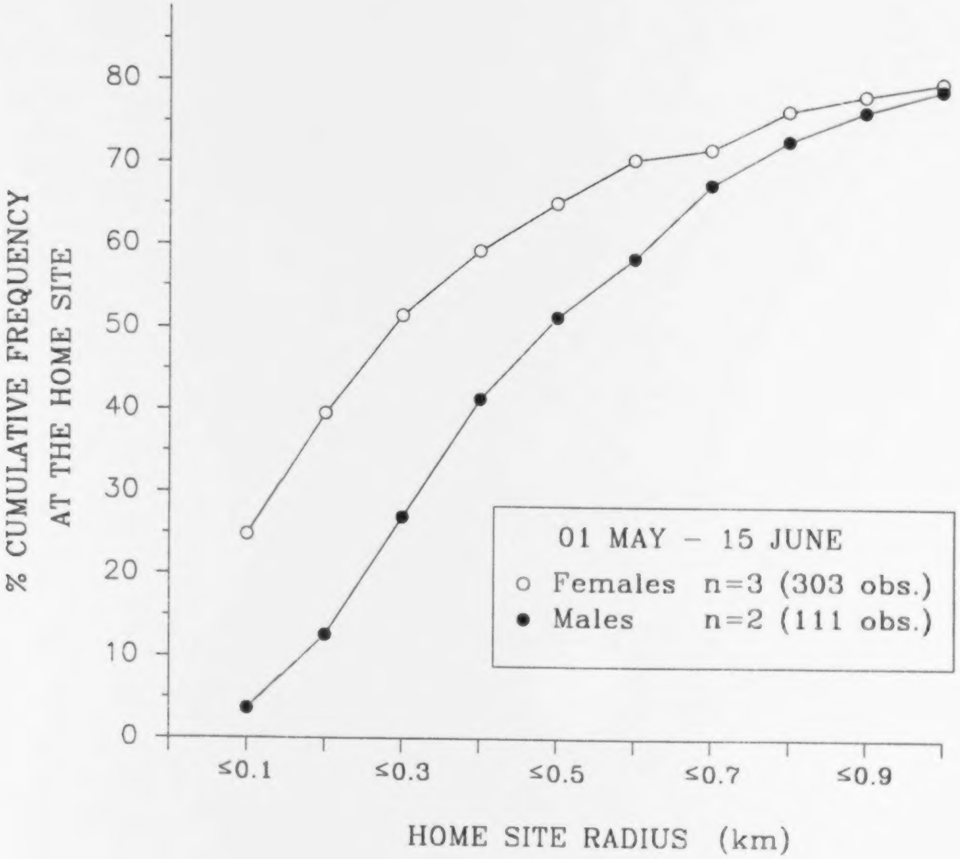

Figure 3–1. Effect of changes in den site radius on the cumulative percent of radio–locations considered at the den site for male and female coyotes during pup–nursing, southwestern Manitoba, 1989–1990. Den attendance for males was significantly different from females (2x10 contingency test, $G_{(9)} = 46.096$, $p < 0.001$).

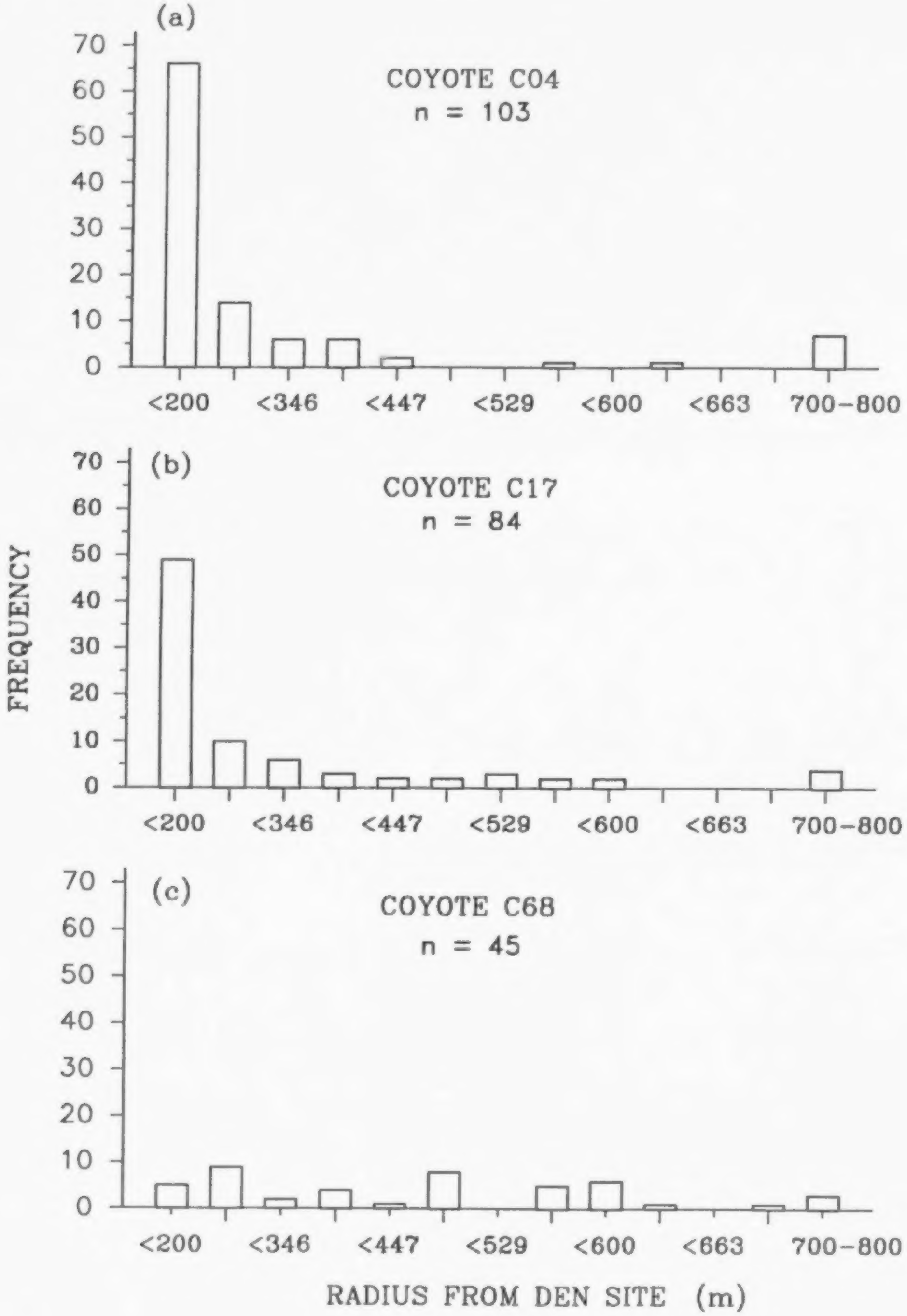

Figure 3-2. Frequency distribution of distances of locations from the den site of adult female coyotes, 01 May to 15 June. Coyotes were radio-tracked in southwestern Manitoba during the summers of 1989 and 1990.

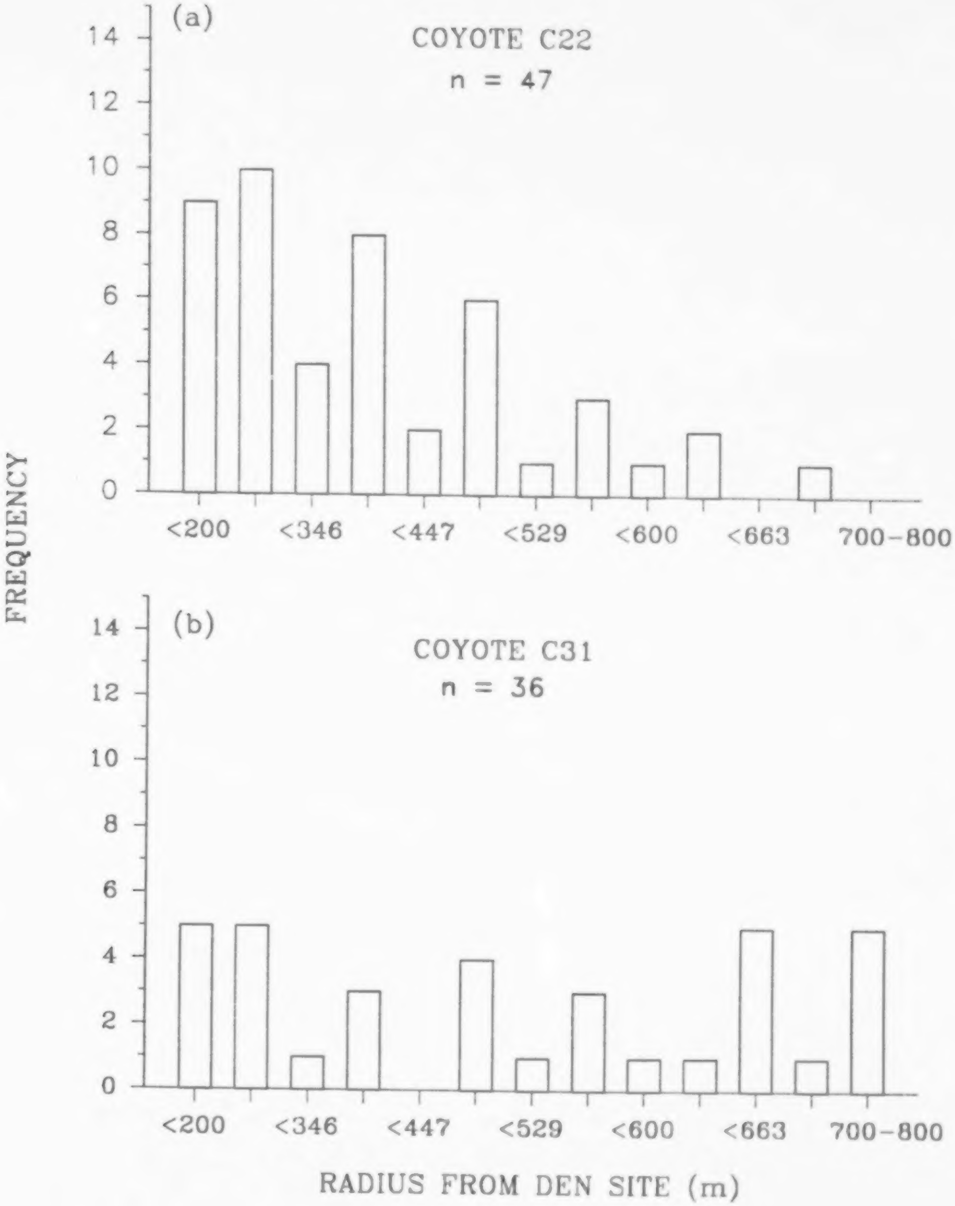

Figure 3–3. Frequency distribution of distances of locations from the den site of adult male coyotes, 01 May to 15 June. Coyotes were radio–tracked in southwestern Manitoba during the summers of 1989 and 1990.

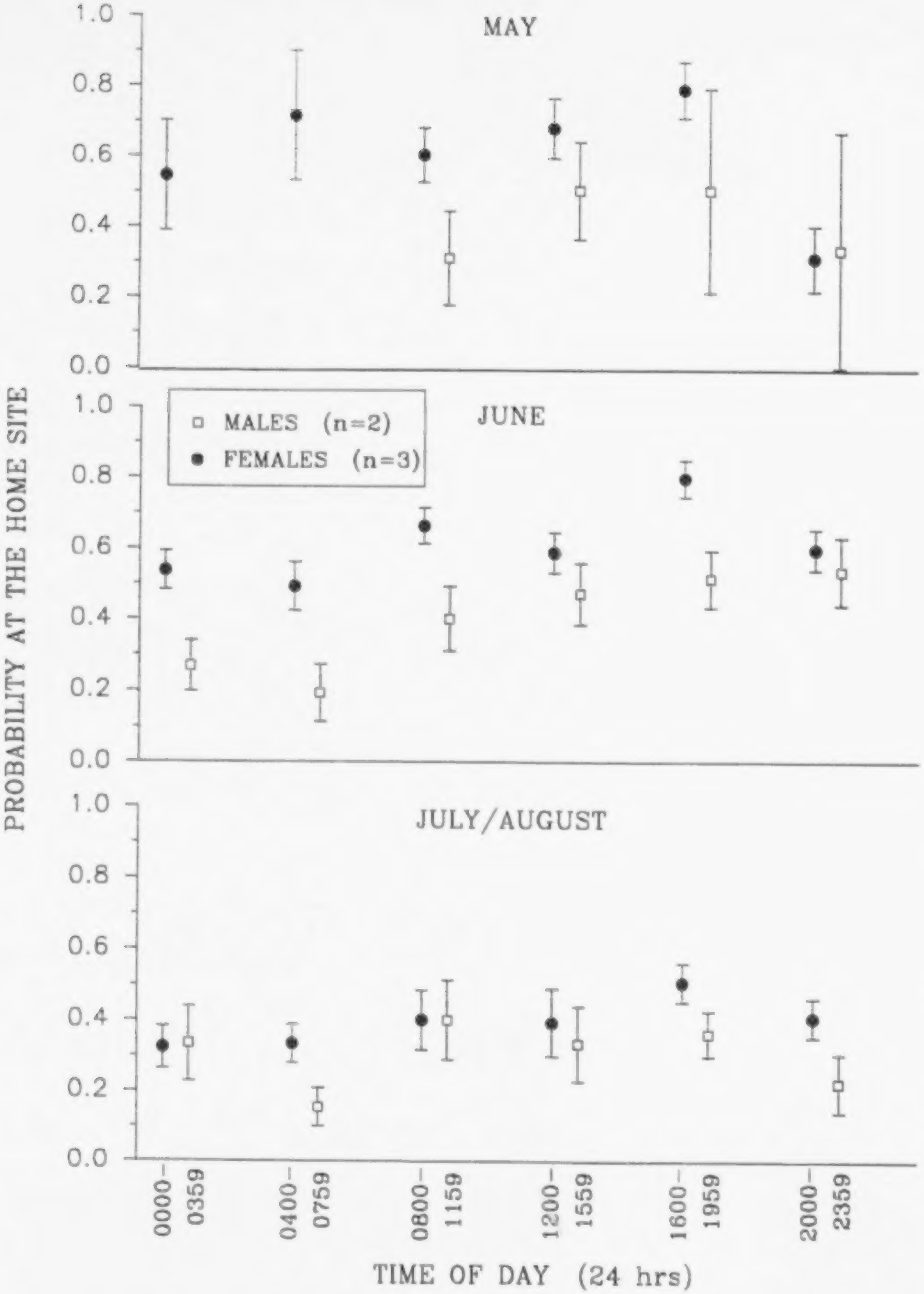

Figure 3–4. Binomial probabilities (±S.E.) of adult coyotes considered at the den or rendezvous site for pup–nursing (May), early post–nursing (June), and late post–nursing (July and August), southwestern Manitoba, 1989–1990.

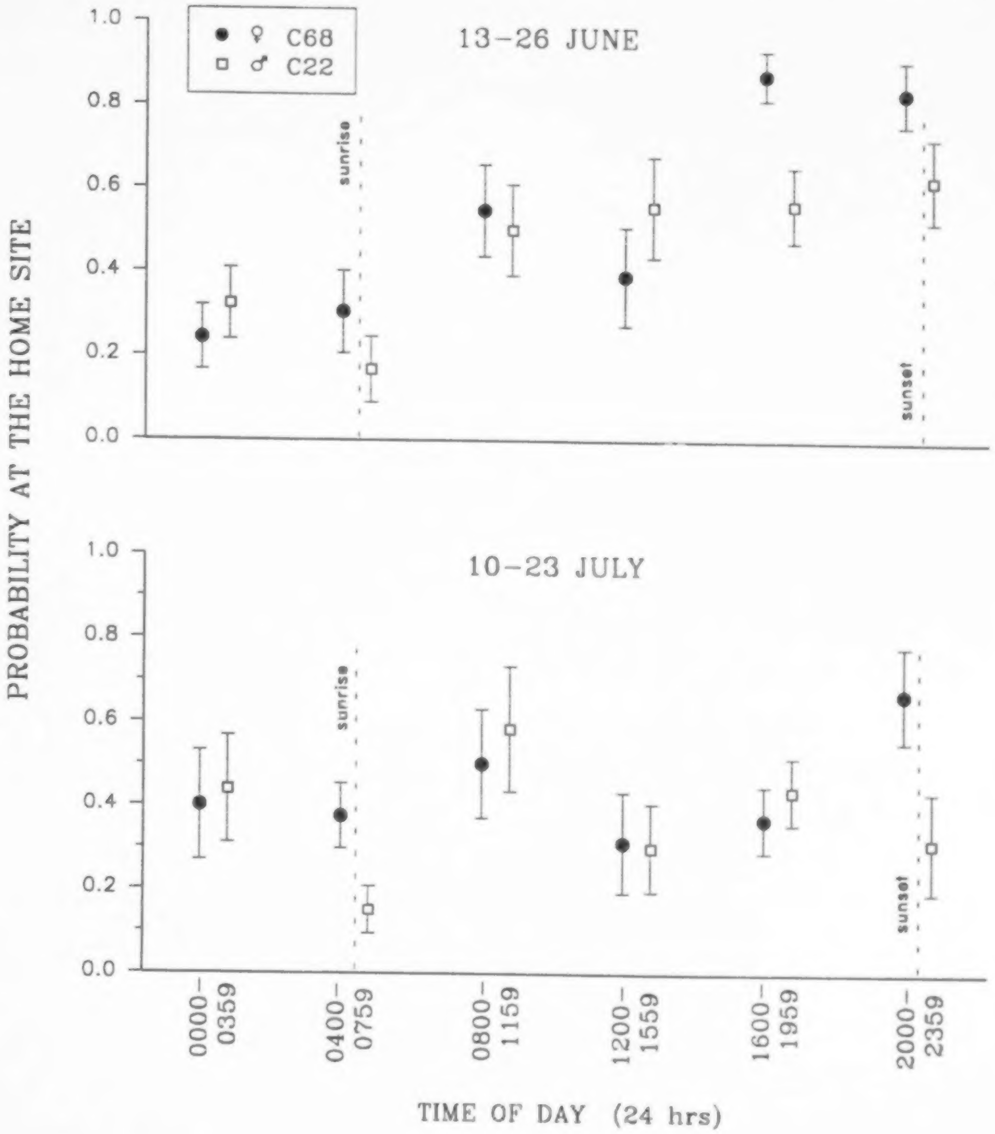

Figure 3–5. Binomial probabilities (±S.E.) of a mated pair of coyotes considered at the den or rendezvous site during sequential monitoring during June and July. On average, sunrise occurred at 0535 hrs and sunset occurred at 2154 hrs. in southweatern Manitoba, 1990. There was no evidence of adult associates helping at the home site.

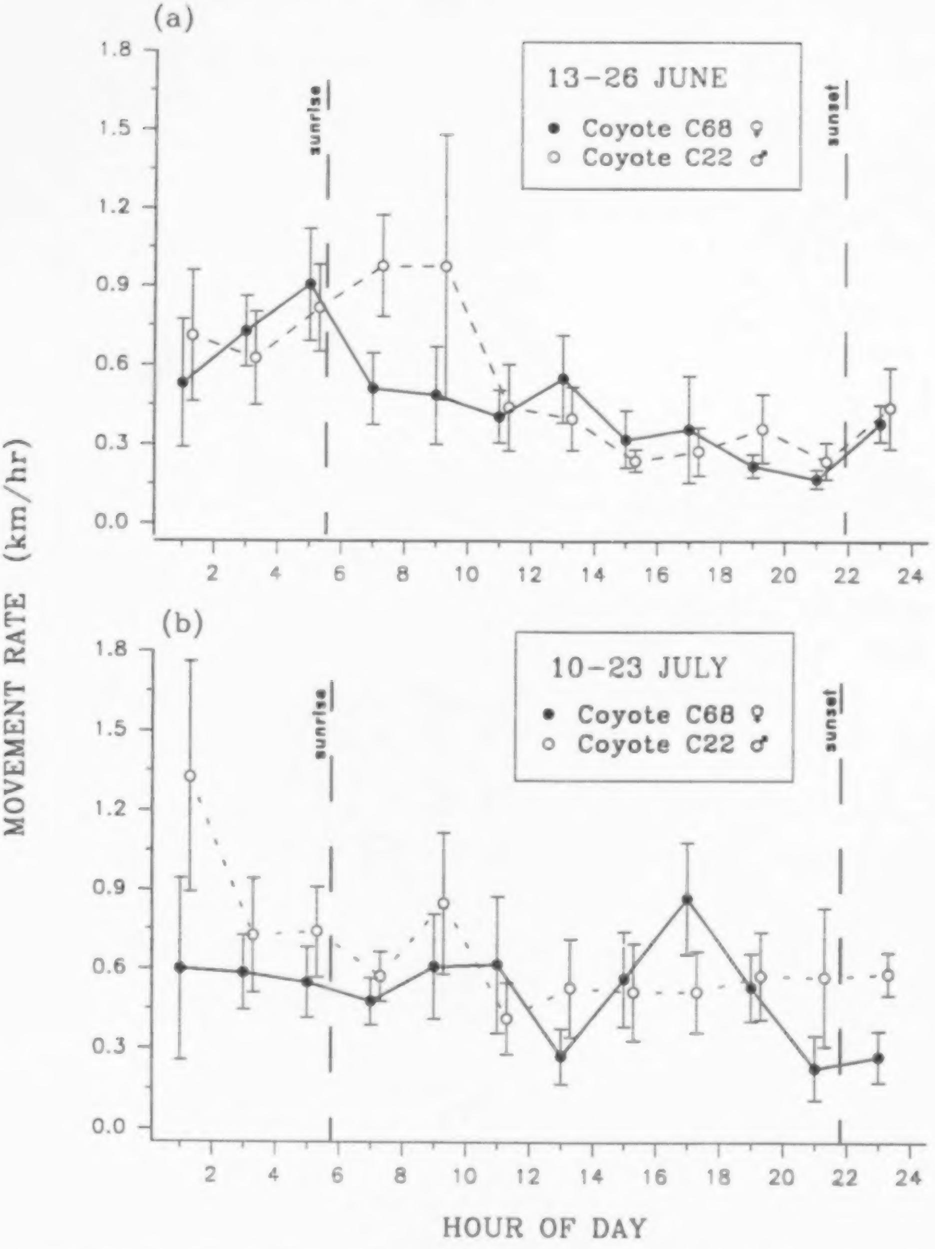

Figure 3-6. Movement rates (±S.E.) of a mated pair of coyotes while away from the den or rendezvous site during sequential monitoring during (a) June (early post-nursing) and (b) July (late post-nursing) in southwestern Manitoba, 1990. There was no evidence of adult associates at the den that may have helped with pup-rearing.

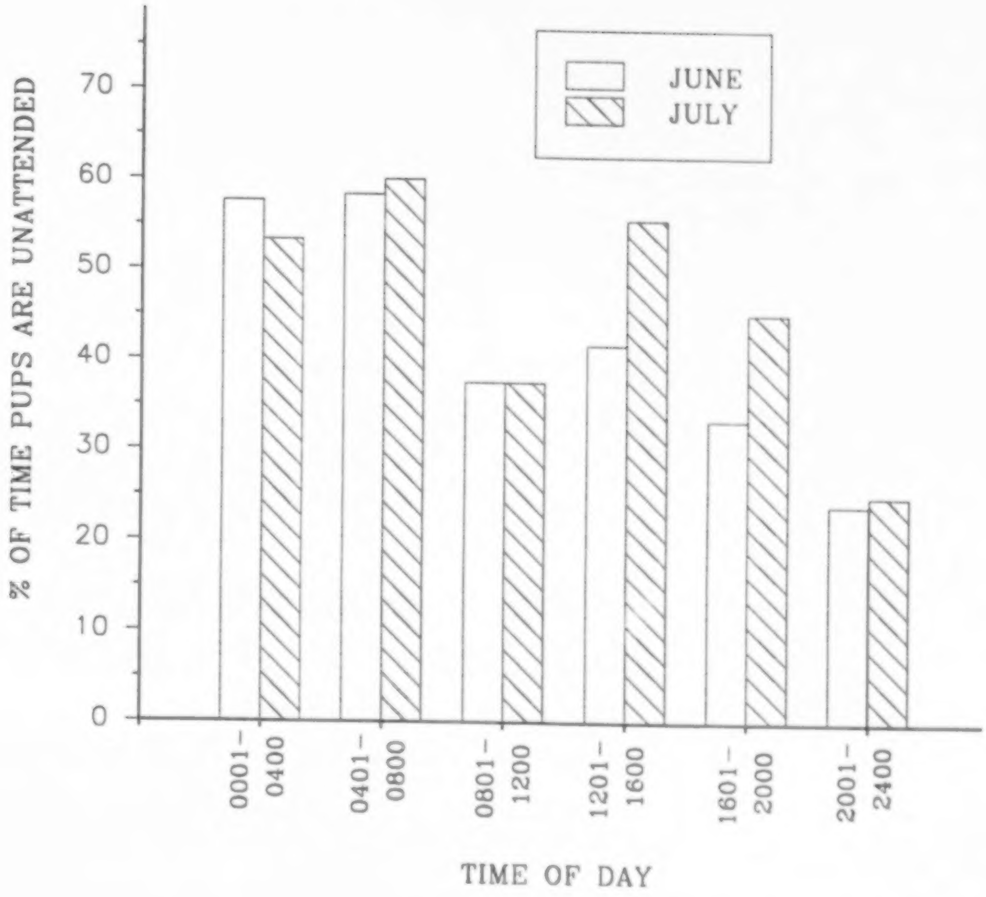

Figure 3–7. Proportion of time pups were left unattended at the home site during June (early post–nursing) and July (late post–nursing) for a mated pair of coyotes, southwestern Manitoba, 1990. There was no evidence of associate adults acting as helpers in pup–rearing.

CHAPTER 4

CARCASS SITE USE BY COYOTES DURING WINTER FOOD ADDITIONS

INTRODUCTION

Food supply acts as a proximate factor in determining an individual's movements, home range size, and possibly resource defense (Boutin 1990). Coyotes are sensitive to changes in their food supply (*e.g.*, Wagner and Stoddart 1972, MacCracken and Hansen 1987, Mills and Knowlton 1991) and show changes in their behavior as available food supply changes. Lindsay (1987) compared reproduction, group size, and behavior of coyotes in two 65 ha enclosures that differed in food availability. Coyotes in the low-provisioned enclosure spent more time exhibiting agonistic behavior (at the carcass and by territorial pursuits among adults), hunting, and at the carcass. These food-deprived coyotes also spent greater amounts of time scent-marking and checking the periphery of the enclosures than coyotes with more abundant food (Lindsay 1987). The influence of food on coyote home range and conspecific intruder pressure, however, could not be examined due to the constraints of captivity. Recently, Mills and Knowlton (1991) examined coyote space use in summer with low and high densities of jackrabbits (*Lepus californicus*). In one of their two study areas, home ranges of coyotes were significantly smaller during a time when prey was abundant. However, there was no difference in home ranges of coyotes under similar conditions at the second site. Mills and Knowlton (1991) suggested that confounding effects of transient coyotes, especially during periods of prey scarcity, may have affected results.

Carrion is a regular component in the diet of coyotes (Camenzind 1978, Bekoff and Wells 1980, 1986). However, the significance of carrion to coyote behavior and ecology has received limited attention. Bekoff and Wells (1982, 1986) examined how winter food availability influenced the behavior and social organization of coyotes by monitoring coyotes in an area of unevenly distributed elk carrion. Where carrion was abundant, clumped, and defendable, packs of coyotes were observed and some juveniles did not disperse during the first year of life. When carrion was scarce and scattered, resident mated pairs and solitary coyotes were observed (Bekoff and Wells 1986). Carcass sites occurred by chance and no attempt was made to control the distribution of carrion (Bekoff and Wells 1980). Bowen (1978, 1981) added food to home ranges of coyotes in the field. He observed coyotes at road-killed ungulate carcasses that he provided in winter. Bowen placed carcasses at the center and edge of coyote territories in anticipation of differences in aggressive encounters from conspecifics (center-edge effects), but he was careful not to create large, predictable sources of food. Consequently, the role of regular carrion sites could not be assessed.

Carcass sites are relatively common in agricultural areas where regular carrion sites may occur near cattle feedyards (*e.g.*, Todd and Keith 1976, Danner and Smith 1980). The significance of agricultural carrion became apparent when Todd and Keith (1976) monitored coyote population responses to reductions in agricultural carrion. Because their efforts were directed at evaluating the removal of carrion availability as a means of coyote population control rather than space use patterns, Todd and Keith (1976) did not consider the influence of resupplying regular carcass sites nor the influence of carcass removal on individuals. However, Todd and Keith (1976) showed that some coyotes do emigrate and perhaps starve if carrion sources are removed.

Danner and Smith (1980) monitored radio-collared coyotes near a livestock carrion site in Arizona for two winter seasons. Immature coyotes were thought to be more dependent on the food site than adults. However, home ranges of all monitored coyotes overlapped with one another and carcass site use suggested enlarged home ranges of adult coyotes but not for pups and yearlings (Danner and Smith 1980). It was not clear if monitored adult coyotes (6 females, 1 male) were transients or residents. Consequently, the influence of location of the carcass site within a home range, whether at the center or edge, could not be determined.

Center-edge effects occur when territorial residents respond more aggressively to intrusions, usually by conspecifics, at the territory center than at the edge (Falls 1982). Center-edge effects have been shown for many birds (*e.g.*, Falls 1982, Giraldeau and Ydenberg 1987) but remain unclear for mammals such as coyotes. Bowen (1981) observed more visitations to carcasses by transient coyotes when the carcass was placed at the territory edge rather than at the center of a home range. He found that transients rarely fed for long periods at carcasses located near the home range center. However, it was unclear whether a resident's behavior towards intruders differed with geographic location within the home range.

Coyotes are usually described as generalists and opportunistic predators (*e.g.*, Todd and Keith 1976, Van Vuren and Thompson, Jr. 1982). However, coyotes have also been described as possible optimal foragers (MacCracken and Hansen 1987) although the evidence remains equivocal (Boutin and Cluff 1989). Whatever their foraging strategy, winter carrion comprises a major component of the coyote diet whenever available (Todd and Keith 1976, Camenzind 1978, Danner and Smith 1980, Bekoff and Wells 1980, 1982, 1986). The availability of this food source may also precipitate seasonal migrations of coyotes from forested areas in summer to agricultural areas in winter (Todd and Keith 1976, Todd 1985). Carrion use by coyotes is apparently less common in summer, possibly because food supply is more abundant in summer than in winter (see Appendix 4 for carrion use by coyotes in summer).

In this study, I examined the influence of carrion sites on coyote behavior. I hypothesized that space use by coyotes is determined by the availability and location of food resources. I expected that coyotes with carcass sites in the center of their activity area would reduce their activity at the home range edge and therefore show a decrease in home range size. Carcass sites located at home range edges may cause a shift in activity and should be consumed more rapidly that when located in the center because of feeding by transients in addition to residents. Consequently, I introduced carcasses to the center and edge of home ranges of radio-collared coyotes and immediately replenished carcass sites whenever consumed. I tried to create large, predictable sources of food. I monitored coyotes that had carcasses provided (experimental) and those with no carcass sites (control) present. Specifically, I addressed the following four questions: What was the extent of carcass use by coyotes? Was carcass use dependent on location of the carcass? Did home range size change with carcass addition? Did visitation by other coyotes to carcass sites vary with sites at home range centers or edge?

METHODS

1. Study Area

The study area encompassed a 150 km^2 region consisting of part of the southern boundary of Riding Mountain National Park (RMNP) in southwestern Manitoba (50° 40' lat., 100° 10' long.), Canada and adjacent lands outside the park boundary. Within RMNP, dominant cover is the boreal mixed-wood forest although the proportion of aspen (*Populus* spp.) to spruce (*Picea* spp.) is greater in the study area than in other areas of the park. Aspen parkland dominated by agriculture completely surrounds RMNP such that the park may act as an ecological island (2976 km^2) of trees (see Appendix 1 for a detailed description of the study area). Radio-collared coyotes commonly traveled in and out of the park. A network of roadways outside RMNP allowed vehicle access for monitoring coyotes no further than 1.6 to 3.2 km away.

2. Capture, Marking, And Monitoring Of Coyotes

Coyotes were captured with No. 3 Soft Catch padded leghold traps (Woodstream Corp., Lititz, PA) primarily during summer but also on an *ad hoc* basis in winter when temperatures were relatively warm (≥ -8°C.). Live-trapping was not permitted inside park boundaries but occurred on the adjacent agricultural area south of RMNP and west of Clear Lake. Captured individuals were classified by sex and age. I estimated age classes by body size and dentition (see Appendix 2 for capture data). Age classes followed Andelt (1985) and Gese et al. (1988) and comprised pups (<9 months old), yearlings (9-21 months), and adults.

Coyotes were monitored on most days during the winters (Dec-Mar) of 1988-89 and 1989-90. Three locations were attempted each day in January-March for coyotes within range of ground vehicle access. Time between consecutive location attempts was approximately 4-8 hours and occurred at all times of the day so as to minimize autocorrelation (Swihart and Slade 1985, Chapter 2). Locations were normally estimated by triangulation from bearings obtained by a hand-held antenna from a ground vehicle. Hand-held antennas were either 2-element (winter 1989) or 3-element antennas (winter 1990). Normally three bearings were taken for each ground-based location estimate although locations based on two or four bearings were also used. The ad hoc method (Nams and Boutin 1991) was used to initially reject locations considered too imprecise. The error triangle technique (Nams and Boutin 1991) formed the basis of estimating an individual's location although the probability of the estimate containing the true location could not be determined (Nams and Boutin 1991). However, reference transmitters at known locations were used to estimate the accuracy and precision of the triangulation procedure using the maximum likelihood estimator (Lenth 1981) provided in the LOCATE II program (Nams 1990). Based on these reference transmitters bearing error was estimated at ±2.0°. I used program HOME RANGE (Ackerman et al. 1990) to estimate home range size and use. Visual observations of coyotes, usually from aerial location attempts, aided as indicators of group associations.

3. Food Additions

I used livestock carrion obtained from local farmers and white-tailed deer (*Odocoileus virginianus*) or elk (*Cervus elaphus*) carcasses from road-kills and other sources to supply carcass sites. Whenever possible, I weighed the carcasses before introducing them to a site. Carcasses were either whole or sectioned during the winter of 1990, depending on the carcass size. No sectioning of carcasses was performed during winter 1989 although some deer carcasses were skinned prior to their deployment. I tried to minimize contact with the carcass at all times. I used a snowmobile to distribute carrion to various sites. I also checked sites by snowmobile and kept to my initial track. I replenished a carcass site whenever carcass consumption was complete or nearly so.

Only adult coyotes with a stable home range area were given supplemental food. I determined the initial home range area by the radio-locations obtained for the current winter prior to any food additions (December to mid-January). The first carcass site was located near the home range centre as determined by the harmonic mean centre (Neft 1966). I adjusted the location of the carcass sites slightly if the level of human disturbance and/or the relative ease of access for monitoring the site was compromised.

4. Carcass Use

I documented coyote activity at carcass sites by tracks in snow, scat depositions, radio-tracking, and visual observation of coyotes that left the site with my approach. I distinguished between activity at carcass sites located centrally within home ranges of coyotes with those situated near the edge. I estimated the area used by monitored coyotes before and during the addition of food to test for changes in home range size. I used the minimum convex polygon (MCP) method (Mohr 1947) to estimate the area used by coyotes. This method is simple, intuitive, and a non-parametric procedure for calculating the area enclosed by a set of locations (Bekoff and Mech 1984, White and Garrott 1990). Although the 100% MCP method is sensitive to sample size and outliers, I selected the 100% contour level for comparison between different time intervals because all areas used during a time period, including sallies, were important. If food supply was limiting and an important factor determining movements of coyotes, I expected the addition of food would reduce activity (*e.g.*, sallies) beyond the normal home range area. I also estimated the area used by monitored coyotes with the harmonic mean method (Dixon and Chapman 1980). This non-parametric method calculates a utilization distribution (Van Winkle 1975, Anderson 1982) by estimating the probability of use at any location in the home range (Dixon and Chapman 1980, White and Garrott 1990). I calculated core activity areas from the harmonic mean method as a second estimate of area used by coyotes because it is less sensitive to differences in sample sizes between comparisons. I checked for any shifts in activity areas when food was added with the harmonic mean center because of its ability to detect large, sudden shifts from an area of high activity to another (Dixon and Chapman 1980). I also calculated the distance from the carcass site for each location. I considered differences statistically significant at the $\alpha = 0.05$ level.

RESULTS

1. Study Animals

Twelve coyotes were monitored during food additions and their home ranges determined (Table 4-1, Fig. 4-1). Coyotes C11 and C17 received carcasses during winter 1988-89. Carcass sites were established for coyotes C04, C22, C23, and C27 during winter 1989-90 (Table 4-1). Two coyotes (C20 and C67) were repeatedly located at another livestock carcass site during winter 1989-90 for about eight weeks beginning in late January (Figs. 4-1, 4-2). During the first winter, coyotes C04 and C08 were monitored as controls. Coyotes C17, C21, and C23 were used as controls during the second winter (Table 4-1). Therefore, two coyotes (C04 and C17) were monitored over two winters and their experimental treatment was switched for the second winter.

2. Extent of Carcass Use

Coyotes visited carcasses at all sites, however carcass consumption by coyotes varied widely (see Appendix 5 for detailed descriptions). I placed carcasses at four sites on 12 January using a domestic cow carcass (estimated at 295 kg) at site W17a and pieces of cattle or deer carcasses at the other three sites. Carcass pieces initially totalled 33-38 kg for each of the latter three sites. Activity from coyotes at three of the four sites did not occur immediately after carcasses were introduced. Tracks in snow from coyotes were first observed at site W17a, at least a week before the other three sites. Consumption of carcasses by coyotes at site W17a followed after another six days. Coyotes did not feed at sites W22a and W27a until mid- to late February, respectively. When coyotes did feed at these carcass sites, complete consumption of carcasses either did not occur (sites W17a, W22a, and W27a) or the carcasses lasted until early April (site W4a). Total amount of food added was 402, 85.5, 305 and 143 kg for sites W17a, W22a, W27a and W4a respectively. Total consumption by coyotes for the first three sites was insignificant. Carcass pieces at site W4a were eventually completely consumed except for hide and scattered bones.

I introduced another four carcass sites between 15-19 February (Appendix 5). This time, I preset a snowmobile trail to the intended carcass site before I added food.

About a week later, a deer carcass weighing between 43-79 kg was added to each site. Tracks from coyotes occurred at each site within 2-6 days after carcasses were introduced. On two occasions (at sites W17b and W22b), a coyote was observed at the carcass site (<100m) although no feeding occurred until several days later (Appendix 5). Coyotes ate all food I initially provided at these four sites but consumption did not occur until 21-27 February or 12 March (site W17b). I discontinued site W17b after 22 March once the two deer carcasses (118 kg in total) were completely consumed. I replenished the other three sites with additional carcasses or carcass pieces. These carcasses were also consumed by coyotes and I subsequently replenished these until early April. At this time, 118, 231.5, 193.5, and 243.5 kg were supplied to carcass sites W17b, W4b, W4c, and W22b respectively. Only hide and bones remained at each site when monitoring ended.

Visits by radio-collared coyotes supported my observations for all carcass sites except site W4c. I recorded two radio-collared coyotes at each of sites W17a and b, W20a, and site W4b based on locations at (≤200m) or near (≤400m) carcass sites (Table 4-2). I observed a third coyote at sites W17a and W4b either on the ground or from the air. Although only one coyote was monitored for sites W22a and b, it was frequently located near the carcass sites (Table 4-2). Tracks in snow were always paired indicating a mate accompanied coyote C22. No locations of radio-collared coyotes were recorded near site W4c although three deer carcasses were consumed.

3. Carcass Use In Relation To Its Location Within Home Ranges

Four of the nine monitored carcass sites were placed in the central portion of home ranges of radio-collared coyotes (Fig. 4-2). Carcasses at two of the centrally located carcass sites (W4b and W22b) were completely consumed (typically, only hide and skeletal columns remained). Tracks from coyotes at site W22a confirmed that coyotes visited the site but did not feed on the carcass. Radio-locations of coyote C22 suggested that C22 was near site W22a (Table 4-2) when food was available. Site W4a was the least used by coyotes among all monitored carcass sites.

The five remaining carcass sites were located on the edge of home ranges of monitored coyotes (Fig. 4-2). Coyotes made frequent visits to sites W17a and W20a although consumption of the cattle carcasses was far from complete (Appendix 5). Tracks from coyotes were observed leading into both carcass sites. Coyotes visited site W20a nightly which resulted in a well-packed snow trail that crossed a road and adjacent field. Radio-locations confirmed daily movements of coyotes to and from the carcass, however, not all visits to the carcass were at night. Both sites W17a and W20a have been supplied with livestock carrion from local farmers in previous years.

Carcass sites W27b and W4c had little or no consumption by resident coyotes, perhaps because the location of these sites approached the outer limit of the coyote's home range (Fig. 4-2). Site W4b may also have influenced visits by coyotes to the west side of the C04 home range. Although site W27a was the only consistent carcass site within coyote C27's home range, gut-piles from elk and moose occurred at irregular intervals as a result of hunting activities. Furthermore, two cow elk were killed illegally to the northwest of site W27a and the carcass was immediately abandoned by the poachers. Consumption of the carcass by scavengers was virtually complete before I discovered them.

4. Carcass Use and Home Range Size

I obtained home range size estimates for the period before and after the addition of food in six cases. None of the areas used by coyotes decreased in size after food was added (Table 4-3). This may have been because the number of locations used to determine home range size between periods were not equal. With equal sample sizes between comparisons, home range size decreased by 2.8 km^2 for only one coyote.

However, a similar decrease (3.7 km^2) also occurred for one control coyote. Home range increased for coyote C27 once food was added and may be because C27 was present in the carcass site area for a short time but it was not a regular area of activity for her.

Core activity areas declined in two cases (coyotes C04 and C27) during the food addition period while core areas increased among control coyotes (Table 4-3). No change in pattern occurred when I made the number of locations equal before and after food addition. However, coyote C27 was seldom located at site W27a so a decrease in core activity area was not due to the carcass site. Consequently, a decrease in home range size before and after adding food was consistent for both area estimators for only coyote C04.

Carcass sites likely influenced shifts in the harmonic mean center of activity. Shifts in the harmonic mean center occurred for all coyotes receiving food supplements except coyote C22 (Table 4-4). Carcass sites for C22 were both considered in the central portion of C22's home range and the influence of the carcass site was uncertain. Site W4a may have caused a shift from the pre-food addition period and Site W4b may have shifted activity from Site W4a. Both shifts in activity centers were greater than one km and were directed about one km closer to the carcass sites (Table 4-4). Site W4c did not attract coyote C04 to the home range edge. The activity center shift occurred in the opposite direction to site W4c and was likely a consequence of site W4b. Three other carcass sites located at the home range edge corresponded with a shift in the harmonic mean center of at least 750m (Table 4-4). For two sites the shift was directed towards the carcass sites. Coyote C17 did not shift her activity to site W17b but may have been influenced by site W17a. Harmonic mean centers of activity did show a pronounced shift (>0.5 km) for three coyotes. However, two of the three shifts occurred when unexpected sources of carrion were discovered. Therefore, not all monitored coyotes acting as controls during winter 1989-90 were completely without carrion for the entire winter.

Coyote C17's and C21's home ranges had three whole cow elk carcasses and several gut piles available as a result of elk being killed during the hunting season (*e.g.*, 02-23 Dec 1989 and 01-20 Jan 1990) and the native Indian harvest, the latter being unrestricted in season but usually occurring after January. At least seven whole elk carcasses resulted from hunters that abandoned antlerless elk shot in the bull-elk-only season. Although one entire elk carcass was removed before any feeding on it occurred, two other carcasses were not discovered until virtually all the meat was consumed. The home range of coyote C31 overlapped with that of C17 and C21 and C31's presence near the elk carcass and shift of its harmonic mean activity center suggests that one carcass was consumed by C31 and its mate. Consequently, one elk carcass was available to coyote C17 and C21 and one carcass to C31 during the otherwise carcass-removal (control) period. I did not recalculate home range estimates that excluded radio-locations during the two periods when a whole elk carcass was believed available to coyotes. The number of locations prior to the food addition with this restriction was less than 20 locations and too small for useful home range estimates.

Distances between where coyotes were located and carcass sites established within their home range were variable and, with one exception, not influenced by food addition (Fig. 4-3). The mean distance between radio-locations of coyote C22 and carcass site W22b was significantly smaller after the carcass was added. No significant difference in distances to carcass site W22a occurred whether or not food was present.

The magnitude of the distances has little significance because it primarily reflects the location of the carcass site within the coyote's home range. However, carcass sites were visited by coyote C17 whom averaged 2.5 to 3 km from the two sites. Variances of distances of coyotes to four carcass sites decreased slightly (Fig. 4-3). Variation in distances increased for coyote C27 when the food site on the edge of her home range was activated. Small sample size (n = 6) likely contributed to the apparent difference in distances to carcass site W17a for coyote C17 rather than the addition of food. Although coyote C27 did not approach site W27a until early March, the pattern of distances from the carcass site remained the same whether or not I extended the period prior to food addition until I suspected coyote C27 became aware of the carcass site.

5. Carcass Location and Visitation By Other Coyotes

Of the four carcass sites centrally located in home ranges, I thought three were used by residents only. The single set of coyote tracks commonly observed at the fourth site (W4a) suggests visits by transient coyotes or repeated visits by a member of the resident group (three coyotes observed). Carcasses located at the home range edge were frequented more by coyotes other than the residents. I could confirm this by radio-telemetry at one site (W20a). Coyote C20 was located over much of the study area before she began using site W20a by mid-January. By the end of March, C20 had dispersed from the carcass site although the first cow carcass and much of a second remained. Coyote C67 was captured near site W20a after mid-March and was seldom located at the carcass.

Carcass sites W4c and W27a were likely consumed by coyotes that were not radio-collared. Resident coyotes were not present at the site when consumption at the carcass occurred. Coyote C11 apparently made use of both sites W17a and W17b. By April, C11 had dispersed from the area and was later killed northeast of RMNP near Rorketon in January 1990, about 90 km from the carcass sites. Site 17a was visited by adult coyote C19 whose movements seldom occurred outside the park except when near site W17a.

DISCUSSION

1. Carcass Site Location and Use

Coyotes did not consume carcasses as expected. Although coyotes visited all carcass sites, their response to the additional food was variable and unpredictable. One possibility is that coyotes were not food-stressed at this time of year. However, if this is true, whether winter is generally not a food-stressed time (*i.e.*, similar to the situtation for wolves), or prey was temporally abundance was not determined. The snowshoe hare (*Lepus americanus*) shows a strong periodicity in numbers (Keith et al. 1984). In RMNP, hare numbers paeked in 1981 and declined until 1985 based on track counts (Poll 1981) each winter (Carbyn et al. 1987). Assuming a 10-year cycle on average, the next peak in hare numbers would be expected in 1991. However, track counts were discontinued after 1990. Based on trend information up to 1990 and anecdotal evidence, hares were abundant during my food addition period. To what extent coyotes preyed on snowshoe hares during this time, however, is not known.

For some carcass sites, coyotes may have been wary of the sudden food source and the accompanying human scent. However, the wariness of coyotes to novel items (*e.g.*, Hibler 1977), if indeed a factor, should gradually wane as must happen when coyotes feed on ungulate 'gut-piles' left by hunters. Consequently, it is not likely that human scent at a carcass would significantly influence carcass use after about a week. However, behavioral differences in response to novel items may vary extensively with each individual such as whether an individual is transient or resident. Social ranking within a group has been shown to influence feeding among coyote pups in the presence of novel items (Johnson and Balph 1990).

Most carcasses were frozen when I added them to home ranges. Consequently, carcass use by coyotes may have been influenced by long handling times required to feed on frozen hide and flesh, especially for large ungulates. Consumption of carcasses was probably facilitated by thawing during late March-early April. The three sites where consumption was not complete by early spring included large domestic cow carcasses where many areas of the carcass were not accessible to coyotes. When a thawed deer carcass was introduced to site W17a, coyotes consumed it in one night.

2. Influence of Carcass Sites

Monitored coyotes did not appear dependent on the food provided and instead likely used the carcass sites to supplement their diet. All monitored coyotes observed (usually during aerial locations) showed no sign of poor health. No mange (from the mite *Sarcoptes scabiei*) was observed although reports of coyotes with hair loss occurred nearby. Because of the indifferent use of carcass sites by coyotes, food supply within the home range was likely not limiting. Consequently, variation in response to the food supply manipulation would be large and difficult to interpret with the sample sizes used here. I also avoided comparing coyotes C04 and C17 over different years because of possible yearly/seasonal effects (Laundré and Keller 1984).

No decreases in home range size were apparent because of my food additions. Although there was a reduced area of use by coyote C04 when carcass sites W4b and W4c were active (17 February to 31 March), the difference may not be significant as no measure of variance exists with the minimum convex polygon (White and Garrott 1990:172). Furthermore, there may have been an increase in area used during the food addition period for those coyotes receiving additional food.

A carcass site should have its greatest influence when it is replenished at predictable rates. Consequently, livestock dumping areas or 'graveyards' have the greatest potential to influence movements. Indeed, carrion removal in central Alberta had dramatic effects on demography of the over-winter coyote population (Todd and Keith 1976). Conversely, ungulate gut-piles resulting from hunters field-dressing their kill is generally unpredictable and ephemeral if the hunting season is short or harvests are small for a protracted season. In Grand Teton National Park, Bekoff and Wells (1980) found that coyotes rely heavily on the availability of ungulate carrion during winter. Although the hunting of elk by humans was limited seasonally, regular, albeit isolated, sources of ungulate carrion were often available throughout winter where elk herd formation occurred (Bekoff and Wells 1980). In the RMNP area, elk and moose (*Alces alces*) are hunted in December and January in most years. Harvest by native Indians extends into February and March usually near the park boundary. However, ungulate gut piles are rapidly consumed, especially by ravens (*Corvus corvax*), and likely do not constitute a significant source of reliable food for coyotes. The significance of gut piles for coyotes may only be a short term benefit that appeases hunger and preserves the individual's strength to acquire the next meal. Feeding at kill sites of other sympatric predators such as wolves (*Canis lupus*) might be a foraging strategy of some coyotes (Paquet 1989). However, following wolves in anticipation of feeding on the carcass of a wolf-kill can prove fatal to coyotes (Paquet 1989, 1991).

Livestock carcasses have always been provided for coyotes at carcass site W17a for C17 each winter and occasionally in summer. For several years, as the accumulation of bones can attest, 2-3 domestic cattle that die nearby have created a predictable source of food. Consequently, visitation by many coyotes should be expected. Indeed, coyote C17 averaged over 2.5 km from carcass site W17a while coyote C19 from further inside RMNP approached the carcass site W17a more than once in winter and occasionally in summer (Fig. 4-1). Unfortunately, other coyotes not associated with residents and that visited carcass sites were not radio-collared. Todd and Keith (1976) and Todd (1985) found that coyotes normally occupying forested habitats may supplement their diet from nearby agricultural areas. Although coyote C19 was captured and radio-collared near carcass site W17a, subsequent visits to the carcass site area suggested that these excursions were sallies beyond her usual home range area. Hibler (1977) hypothesized that coyotes may avoid the area of their capture and possibly shift their home range.

Danner and Smith (1980) located radio-collared coyotes that visited their cattle carcass feedyard up to 15.3 km from the carcass site. From these movements and displacement of glass beads originally inserted in cattle carcasses and later recovered in coyote scats, Danner and Smith (1980) estimated their carcass site influenced the coyote population in a 380- to 700-km^2 area. However, Danner and Smith (1980) do not indicate the influence of transient coyotes on their estimate. Resident and young/transient coyotes must be distinguished from each other because of expected differences in their behavior. Residents, by definition, show fidelity to a given area and consequently have stable home ranges relative to transient coyotes. Danner and Smith (1980) believed that immature coyotes were more dependent upon carrion than adults. Consequently, the area of influence that a carcass might have would likely be smaller for resident adults than transients. If regular sources of carrion only significantly affect the mobile cohort of the winter coyote population as Todd and Keith (1976) suggest, the overall distribution of resident coyotes would be virtually stable with respect to food supply. In this study, pups or yearlings at carcass sites dispersed by April but may have done so earlier if no food was present.

Future studies that manipulate the food supply available to coyotes to investigate proximate causes of behavior need to overcome many of the logistical constraints of studying coyote ecology. Consideration must be given to the nature of the food supply, be it clumped or distributed, and whether large carcasses should comprise the food source. That coyotes utilize carcasses is given, however, the high handling cost inherent for a large frozen carcass before consumption by coyotes requires further attention. Technological advancements such as automated radio-tracking and remote photography will likely reduce logistical costs and open other opportunities that address current limitations to monitoring coyotes. However, I expect that coyotes are fundamentally opportunistic and inquisitive individuals such that they would not rely on a small number of sites for food. Rather than relying solely on several predictable carcass sites, coyotes may continue to peruse their home range and beyond for potential food. Furthermore, other behaviors such as scent-marking activity may assume a larger role if food supply became superabundant (Davies and Houston 1984). Consequently, I do not expect that tighter monitoring schedules or increased food supplements would necessarily result in dramatic changes in resident home range size or lack of predation on other prey such as deer.

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Table 4-1. Radio-collared coyotes used in food supply manipulations near Riding Mountain National Park (RMNP) area, Manitoba, Canada, winters (Dec-Mar) 1988-89 and 1989-90.

Coyote	Sex	Age Class at Capture	Capture Date	Winter 1989	Winter 1990	Comments
88-C04	F	adult	17 Jul 1988	control	food added	
89-C23	M	yearling	14 Jul 1989	--	food added	associated with C04
89-C22	M	adult	14 Jul 1989	--	food added	
89-C27	F	yearling	17 Aug 1989	--	food added	mostly inside RMNP
88-C11	M	yearling	15 Aug 1988	food added	--	monitored with C17 in 1989
88-C17	F	adult	12 Oct 1988	food added	control	
89-C21	F	yearling	21 May 1989	--	control	monitored with C17 in 1990
89-C31	M	adult	26 Aug 1989	--	control	
89-C20	F	pup	28 Jan 1989	--	--	C20 & C67 monitored regularly
89-C67	M	yearling	17 Mar 1990	--	--	at a traditional carcass site
88-C08	M	adult	31 Jul 1988	'control'	--	completely inside RMNP

[1] pup (<9 months of age); yearling (9-21 months); adult (>21 months).

Table 4-2. Percentage of locations of radio-collared coyotes near introduced carcasses monitored during winters 1988-89 and 1989-90, southwestern Manitoba. Percentages are given for each carcass site when activated with food and before another carcass was introduced later, if applicable. Letters in parentheses indicate whether the carcass site was located in the center portion (c) or near the edge (e) of the home range.

	DISTANCE FROM CARCASS SITE			
CARCASS SITE	≤200m	≤400m	n	TIME PERIOD
WINTER 1988-89				
Site W17a (e)	8.2	14.1	85	12 Jan 89 - 19 Feb 89
	7.0	12.3	171	12 Jan 89 - 31 Mar 89
Site W17b (e)	1.7	8.3	121	19 Feb 89 - 31 Mar 89
WINTER 1989-90				
Site W4a (c)	0	2.3	86	24 Jan 90 - 17 Feb 90
	0	1.0	193	24 Jan 90 - 31 Mar 90
Site W4b (c)	3.5	9.7	113	17 Feb 90 - 31 Mar 90
Site W4c (e)	0	0	113	17 Feb 90 - 31 Mar 90
Site W22a (c)	1.8	14.5	55	20 Jan 90 - 16 Feb 90
	0.8	6.7	120	20 Jan 90 - 31 Mar 90
Site W22b (c)	10.3	44.1	68	16 Feb 90 - 31 Mar 90
Site W27a (e)	0	3.9	51	20 Feb 90 - 31 Mar 90
Site W20a (e)	17.3	30.6	98	01 Feb 90 - 31 Mar 90

Table 4-3. Estimated area (km^2) occupied by radio-collared coyotes before and during the addition of food to regular sites within the home range area during winters 1988-89 and 1989-90, southwestern Manitoba. The 100% minimum convex polygon (MCP) was used to estimate entire area occupied while the harmonic mean (HM) method was used to calculate core activity areas. Sample sizes (n) are indicated. Coyotes C11 and C17 received food supplements during winter 1988-89 while coyotes C04, C22, and C27 received food supplements during winter 1989-90. Coyotes C04 and C08 did not receive food supplements during winter 1988-89 while coyotes C17, C21, and C31 acted as controls during winter 1989-90.

TIME PERIOD	METHOD	FOOD-ADDED					CONTROL				
		C11	C17	C04	C22	C27	C04	C08	C17	C21	C31
Before food addition	MCP	n/a[†]	n/a	14.6	4.2	6.7	8.3	0.7	13.2	12.9	9.5
	HM	-	-	13.2	1.3	5.2	13.2[‡]	5.5[‡]	5.1	5.3	3.1
	n	6	4	35	34	82	9	4	38	40	28
During food addition	MCP	9.3	20.6	16.8	9.7	18.9	26.8	27.2	15.0	70.7	25.5
	HM	3.0	16.8	10.4	5.3	2.9	13.2	16.4	9.8	27.6	18.1
	n	97	79	105	121	53	96	69	110	110	145
First food site active	MCP	8.5	16.3	16.3	6.7	same	23.7	26.2	9.7	9.1	25.5
	HM	0.9	12.9	9.8	4.8		10.4	14.8	5.8	3.8	8.2
	n	53	36	68	56		54	40	71	71	116
Second food site active	MCP	5.3	18.0	12.4	7.7	n/a	24.1	16.5	11.3	70.7	22.4
	HM	2.2	18.2	8.4	4.2		23.7	8.7	8.5	21.9	14.6
	n	47	46	60	65		44	30	64	64	67

[†] not available or applicable.

[‡] not a core area because sample sizes ≤10 locations preclude its calculation.

Table 4-4. Change in harmonic mean centers of activity when a carcass was added to the home range of a coyote. Letters in parentheses indicate whether the carcass site was located in the center portion (c) or near the edge (e) of the home range. The relative change in distance from the activity center to the carcass site is also given (+ equals an increase in distance).

COYOTE	CARCASS SITE[†]	CHANGE IN ACTIVITY CENTER (km)	CHANGE IN DISTANCE TO CARCASS SITE (km)
C17	W17b (e)	1.71	+ 0.80
C11	W17b (e)	0.76	- 0.20
C04	W4a (c)	1.12	- 0.98
	W4b (c)[‡]	1.22	- 0.95
	W4c (e)[‡]	1.22	+ 1.11
C22	W22a (c)	0.39	+ 0.32
	W22b (c)	0.21	- 0.16
C27	W27a (e)	0.78	- 0.50

[†] insufficient number of locations for coyote C20 before its activity at site W20a.

[‡] carcass sites introduced at the same time.

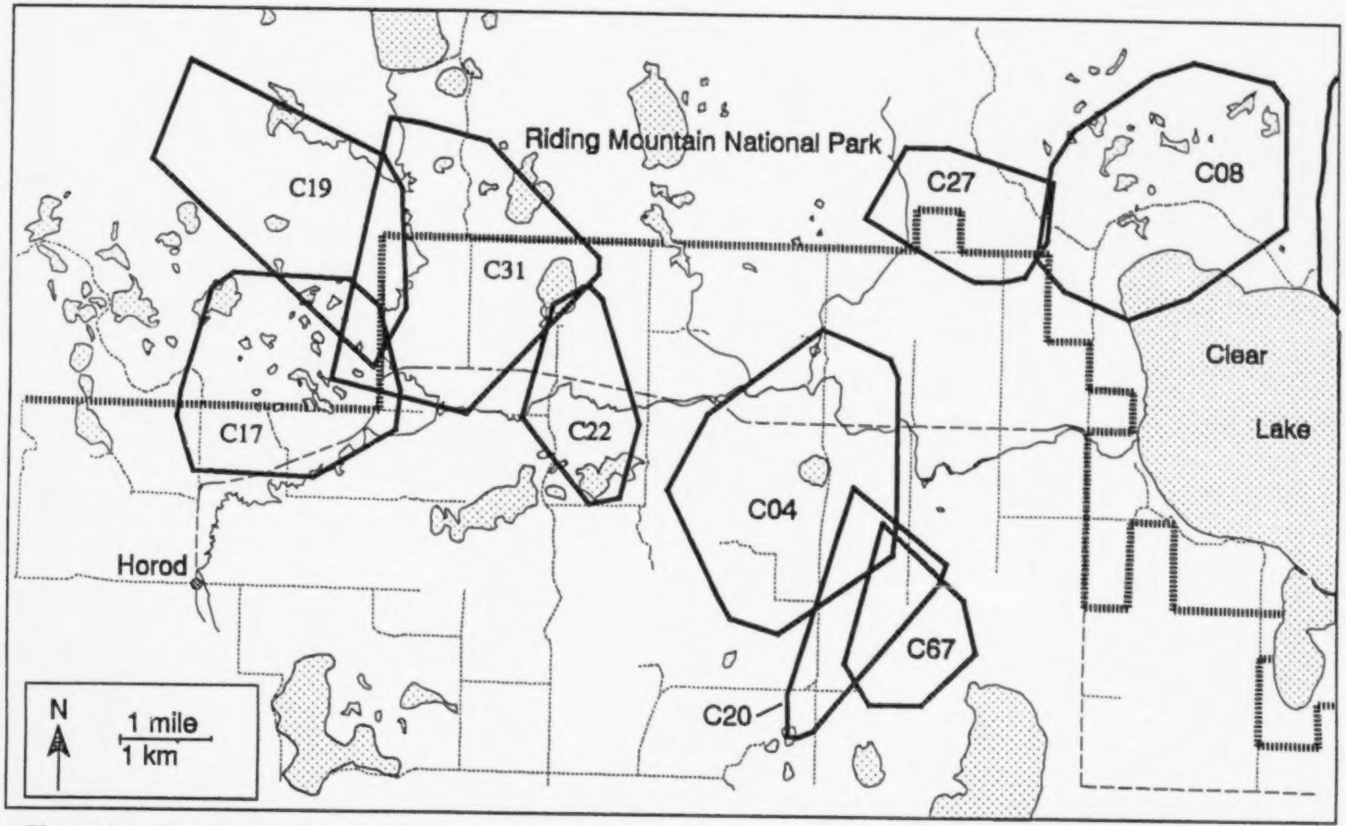
Riding Mountain National Park
C19
C31
C17
C22
C27
C08
C04
C67
C20
Clear
Lake
Horod
N
1 mile
1 km

Figure 4-1. Composite winter home ranges of radio-collared coyotes in southwestern Manitoba, 1988-1990, as estimated by the 95% minimum convex polygon method. Not illustrated are coyote C05 (northwest of the study area), C23 (associated with C22), and C11, which occupied a similar area as coyote C17.

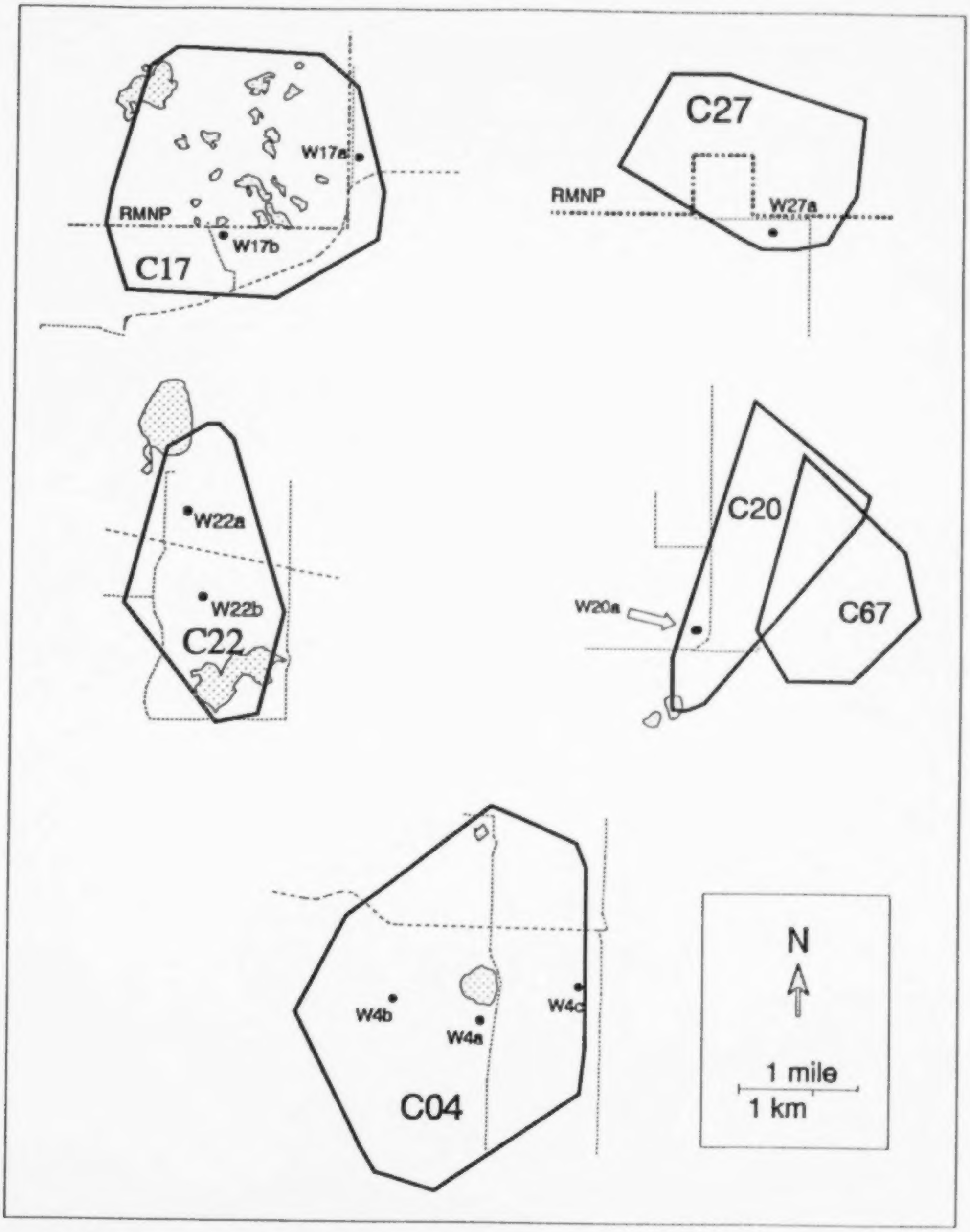
C17
W17a
RMNP
W17b
C27
RMNP
W27a
W22a
W22b
C22
C20
W20a
C67
W4b
W4a
W4c
C04
N
1 mile
1 km

Figure 4-2. Relative locations of 9 carcass sites to home range boundaries of coyotes monitored during food addition in the Riding Mountain National Park (RMNP) area, southwestern Manitoba, during winters 1988-89 and 1989-90. Home range boundaries are estimates by the 95% minimum convex polygon method. Home ranges of coyotes C04 and C17 are composites from both winters. Bodies of water and secondary roads are also mapped.

CHAPTER 5

GENERAL DISCUSSION

I examined movements of coyotes in summer and winter in relation to two biological attraction points (Don and Rennolls 1983). In summer, coyotes involved with pup-rearing must return to a den or rendezvous site to attend their pups. I also tried to introduce other attraction sites in summer by introducing carcasses near active den sites. There is no *a priori* reason to assume biological attraction points occur within home ranges of coyotes in winter. Coyotes do not appear to return to a given site repeatedly over a short time in winter as occurs for a den site in summer. Consequently, I tried to create attraction sites in winter by providing a continual supply of food at specific sites within home ranges of coyotes.

Den and rendezvous sites force coyotes involved in pup-rearing to become central-place foragers where each foraging session of the parents ends with a return to their pups. Both parents participate in pup-rearing activities but differ in approach, at least until mid-summer once pups are weaned. I found that males spend over half of their time away from the den site while females spent >50% of their time with pups. By July, males and females spend an equal amount of time away from the den but still do not seem to hunt together. Consequently, the amount of time pups were left unattended at the den or rendezvous site increased as summer progressed. Distances traveled on excursions also increased from May to August. There was no obvious strategy of parents alternating excursion from the home site. If the time that pups are left unattended at the home site is minimized, I could not disclose it with my monitoring. Although I did not detect any associate adult coyotes serving as helpers for the mated pair I monitored, the presence of a helper may influence the time parents' allocate at the den. However, in one study (Bekoff and Wells 1986), the presence of helpers did not influence the proportion of time that a pack mother spent at the den site.

I found that carcasses I provided had an influence on coyote movements, albeit a small one. Coyotes visited carcass sites at variable rates but nevertheless, the increased presence of coyotes near carcass sites instead of elsewhere likely caused a shift in harmonic mean centers of activity in three, and possibly five, coyotes. However, I only recorded one decrease in home range size when food was added. Criticisms common to home range studies have been concerned with the lack of biological interpretation given to home range size and shape (*e.g.*, Sanderson 1966, White and Garrott 1990). However, the inability to correlate home range size with biological and ecological factors may be due to inconsistent methodology (Smith et al. 1981). I show that two home range estimators can provide very different estimates of home range size even when critical assumptions of each method have been met. Consequently, it is prudent to include more than one measure of home range size and space use when testing predictions that depend on changes in these parameters.

Space use by coyotes is influenced by several factors. Differences in prey abundance can precipitate changes in home range size and shape (*e.g.*, Mills and Knowlton 1991). Therefore, my provisions of carcasses may not have simulated a food supply increase as I had hoped. Golden jackals (*Canis aureus*) have shown small territory size (0.1 km^2) when a concentrated food site is regularly provisioned (Macdonald 1979). However, habitat and habitat use also influence movements of coyotes. Coyotes can select habitat type based on the abundance of prey (Theberge and Wedeles 1989), ease of travel (McKinlay 1990, Murray and Boutin 1991), or other benefits such as exposure to solar radiation when bedded (McKinlay 1990). Messier and Barrette (1982) argued that territorial behavior of coyotes (and therefore space use) is a year-round strategy directed to increase pup survival. Because pup survival is heavily influenced by the ability of parents to obtain food, Messier and Barrette (1982) contend that maintaining territories enhances food acquisition throughout the year. Consequently, the effect of manipulating one factor alone may be concealed by other contributing factors of space use. Finally, coyotes may simply be inquisitive and opportunistic foragers such that this behavior results in frequent visits to most areas within their home range in a given season and may explain their tendency to occasionally venture beyond home range boundaries (*e.g.*, Linsdale 1946:39).

Whether coyotes experience greater food stress in summer or winter remains unclear. Messier and Barrette (1982) observed that breeding males and females captured in summer were always emaciated. Gier (1968) reported malnutrition in pups, a condition also documented among wolves (Van Ballenberghe and Mech 1975). Although food availability appears critical during the pup-rearing season (Messier and Barrette 1982), coyotes were indifferent to carcasses added to nearby den sites. Food addition in summer is further confounded by other scavengers such as black bears (*Ursus americanus*) and rapid decomposition by warm temperatures and insects. Only one deer carcass I provided in summer was consumed by coyotes. In this case, consumption occurred in one night and immediately after I had added it. Therefore, coyotes may use a carcass in summer if decomposition is not advanced. Consequently, attempts to augment the food supply available to coyotes in summer will not likely succeed if only carcasses are added. However, baiting coyotes with carcasses is still feasible if the objective is to initially attract individuals to a specific area. Repeated visits to the site, however, may not occur or be too infrequent for any other practical use.

Bekoff and Wells (1986) acknowledged that coyotes exhibit wide intraspecific variation in social behavior and social organization. This variation would allow analysis of behavioral patterns as phenotypic adaptations to local conditions and consequently they considered coyotes were ideal animals to study in this manner. However, testing hypotheses concerning behavioral and ecological questions require strict control over many variables and coyotes have been less than ideal animals when logistics of controlled experiments in the field are considered. Indeed, in this study coyotes showed wide variation in behavior toward changes in food supply and teasing apart relevant competing variables would require significant logistical costs. However, much of the logistical problems relate to coyote capture and monitoring. Because coyotes tend to be aloof and elusive to capture, perhaps partly due to widespread exploitation by humans, certain individuals from a specific area of interest may not be trappable. These concerns compromise efforts where density estimates, intruder pressure from conspecifics, and repeated examinations through recaptures are required. Consequently, techniques that will facilitate the humane capture and monitoring of coyotes will serve to enhance our ability to study coyotes and increase our understanding of their ecology and behavior.

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APPENDIX 1

DETAILED DESCRIPTION OF THE STUDY AREA

The study area encompasses a 300 km^2 region that includes part of the southern boundary of Riding Mountain National Park (RMNP) west of Clear Lake and Onanole, Manitoba (Fig. A1-1). Located in southwestern Manitoba, 225 km northwest of Winnipeg and 177 km north of the International Boundary between Manitoba and North Dakota, RMNP is a 2976 km^2 area of natural wildland comprised of forested low hills and catchment basins (Trottier et al. 1983). Farmland completely surrounds the 355 km perimeter of RMNP and ongoing land use changes adjacent to the park boundary have increasingly isolated the park as a wilderness island (Trottier et al. 1983). The town of Wasagaming is the only urban area inside the park and functions as the centre for park operations.

The park comprises three major vegetation zones; the boreal and eastern hardwood forests to the north and the prairie grasslands to the south (Trottier et al. 1983, Paquet 1989, 1991). A prominent feature of RMNP is that part of the Manitoba Escarpment which rises abruptly 427m above the surrounding plain along the eastern edge of the park (Trottier et al. 1983). Average elevation in the park is 610m while ranging from 319m to 756m on the escarpment (Trottier et al. 1983).

Vegetation throughout RMNP reflects its history of disturbance from human activities such as logging, livestock grazing, haying, homesteading, and wildfire (Trottier et al. 1983) primarily before receiving official national park status in 1933 (Carbyn 1989). Dominant cover types include aspen-poplar (*Populus* spp.) forest, mixed coniferous (*e.g.*, *Picea* spp. and *Abies* sp.) forest, interspersing sedge (*Carex* spp.)-willow (*Salix* spp.) wetlands, and upland fescue (*Festuca* spp.) prairie (Trottier et al. 1983, Paquet 1991). Detailed vegetational accounts of RMNP are provided by Bailey (1968), Trottier et al. (1983), and Parks Canada (1984).

Agriculture is the dominant land use surrounding RMNP. Most agricultural activities have centered around cereal farming and cattle grazing (Carbyn 1989) although sheep raising and outfitting services for hunting and hiking may also occur. Aspen-popular woodlots are common and variable in size. Large wooded areas usually consist of rolling topography or other impediments to agricultural development.

The climate of the RMNP area is characteristically interior continental climate of the Canadian prairies (Carbyn 1980) with long, cold winters and short, hot summers. January in Wasagaming (elevation 622m) has been the coldest month, averaging a daily temperature of -20.7°C. from adjusted normals from 1951 to 1980 while July has been the warmest at 16.2°C for the same period (Atmospheric Environment Service 1982). Recently, January temperatures have averaged -18.4° and -15.3°C. in 1988 and 1989 respectively in nearby Dauphin (elevation 304m). (Official winter weather records were not available for Wasagaming). July temperatures have averaged 19.5° and 21° for 1988 and 1989 respectively (Atmospheric Environment Service, Environment Canada, Dauphin, MB). Summer temperatures are noticeably cooler in the park (mean July temperatures about 20°C.) and wind chills may also be lower than the surrounding prairie. Microclimates are common in the eastern Escarpment where the topography lends itself to generating updrafts from the lowlands (Paquet 1989). Snowfall may be expected from October to May but accumulations do not become significant until December. However, snow cover persists for five months (mean= 152 days) (Keck 1975). Snow depths vary with topography and vegetative cover in the park but usually do not exceed 50 cm (Paquet 1989).

Elk (*Cervus elaphus manitobensis*) and moose (*Alces alces*) are indigeneous to RMNP and are common throughout the park. White-tailed deer (*Odocoileus virginianus*) have virtually replaced the native mule deer (*Odocoileus hemionus*) (Shoesmith 1976), and frequent the park periphery and agricultural areas outside the park, especially in winter, but are less common in the park's interior (Paquet 1989).

Bison (*Bison bison*) apparently occupied the park seasonally prior to European settlement (Green 1933, Bird 1961) but are now confined to a 532 ha enclosure north and east of Lake Audy. Park objectives seek to maintain a herd of 20-40 bison to maintain a balance with the available food supply (Parks Canada 1980). Beaver (*Castor canadensis*) have undergone an extreme fluctuation in numbers since the turn of the century (Trottier 1980) and have had undesirable economic consequences at high densities (Goldsmith and Rounds 1979).

Wolves (*Canis lupus*) are the dominant predator in RMNP and prey on elk, moose and deer (Carbyn 1980, 1983) while beaver are seasonally important (Meleshko 1986). Coyotes, and perhaps black bears (*Ursus americanus*), are the dominant predators outside RMNP as wolves never venture far beyond the park boundary before returning to the sanctuary of the park (Carbyn 1982, Carbyn et al. 1987). Hunting and trapping of coyotes and wolves are permitted outside RMNP but harvests generally fluctuate with the economy. Red foxes *(Vulpes vulpes*) are rare in RMNP but are abundant outside the park due to agricultural development. Lynx (*Lynx canadensis*) are also present in RMNP and follow the cyclic fluctuations of snowshoe hare (*Lepus americanus*). The endangered eastern cougar (*Felis concolor*) may occur in RMNP in very small numbers but evidence is restricted to the occasional and unconfirmed sightings reported by park visitors (Hoggins 1989). Further accounts of species inhabiting the RMNP are found in Soper (1953a, 1953b).

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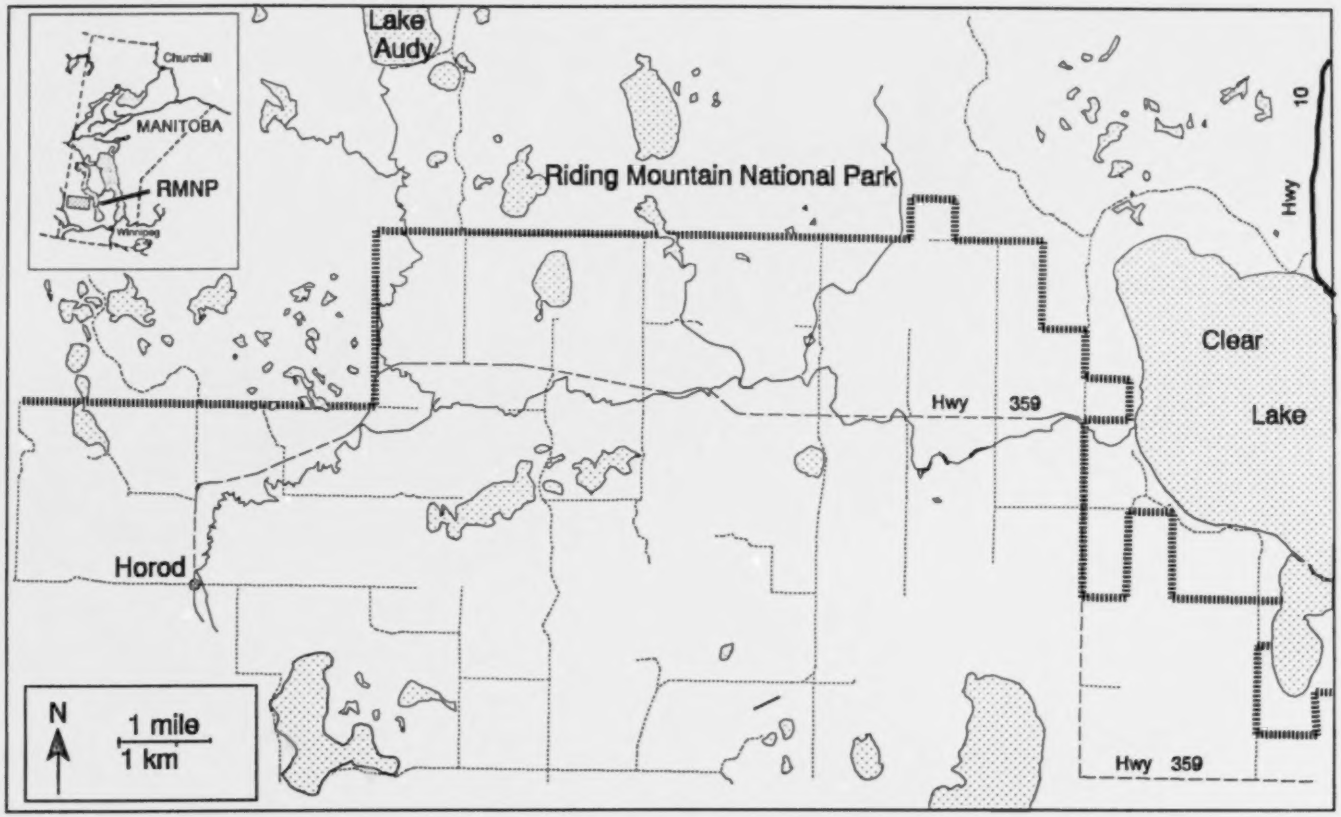
Churchill
MANITOBA
RMNP
Winnipeg
Lake Audy
Riding Mountain National Park
Hwy 10
Clear Lake
Hwy 359
Horod
Hwy 359
N
1 mile
1 km

Figure A1-1. Map of the study area for monitoring coyotes in southwestern Manitoba, 1988-1990.

APPENDIX 2

COYOTES CAPTURED IN THE RIDING MOUNTAIN NATIONAL PARK AREA DURING THE STUDY PERIOD

Table A2.1. Radio-collared coyotes captured in the Riding Mountain National Park (RMNP) area, Manitoba, Canada, 1988-1991. Matrilines follow Lehman et al. (1991).

Coyote	Sex	Age Class at Capture [1]	Frequency (150.xxx)	mtDNA matriline	Capture Date	Last Date of Contact	Last Location (military UTM)	Comments
88-C04	F	adult	.459		17 Jul 1988	17 May 1991	MM 207 131	visual- with 1 other coyote near den
88-C05	M	adult	.480		27 Jul 1988	17 May 1991	LM 992 260	visual on 20 February (single)
88-C07	M	pup	.400	15	22 Jul 1988	24 Mar 1989	MM 166 124	silent radio-collar
88-C08	M	adult	.677		31 Jul 1988	≤12 Jul 1989	MM 291 176	roadkill on Hwy 10 (RMNP)
88-C09	M	pup	.420	3	05 Aug 1988	~30 Nov 1988	MM 211 062	trapped; pup of C17
88-C10	M	pup	.940	3	10 Aug 1988	~Dec 1988	~MM 118 158	trapped; pup of C17
88-C11	M	yearling	.309	3	15 Aug 1988	31 Jan 1990	Rorketon, MB	trapped (near 27-27-15)
88-C12	M	adult	.329		15 Aug 1988	05 Sep 1988	MM 164 331	silent radio-collar
88-C13	F	adult	.431	15	18 Aug 1988	~09 Dec 1988	~MM 232 157	shot
88-C14	M	yearling	.030	2	20 Aug 1988	04 Mar 1990	~MM 020 115	shot
88-C15	M	yearling	.157	3	26 Aug 1988	07 May 1989	MM 109 164	silent radio-collar
88-C16	M	pup	.599	13 or 3	27 Aug 1988	≤15 Jan 1990	MM 060 171	slipped off radio-collar; pup of C17
88-C17	F	adult	.349	3	12 Oct 1988	20 Feb 1991	MM 078 167	shot ≥ February 1991
89-C18	M	[illegible]	.420		14 Jan 1989	05 Feb 1989	MM 236 196	silent radio-collar; front leg missing?
89-C19	F	adult	.959		18 Jan 1989	17 May 1991	MM 090 194	
89-C20	F	pup	.979		27 Jan 1989	07 May 1990	MM 343 080	died ≤ April 1991; l. front paw gone
89-C21	F	yearling	.658		21 May 1989	30 Aug 1990	MM 071 147	associated with C17
89-C22	M	adult	.899		14 Jul 1989	20 Feb 1991	MM 156 138	mate of C68; dead ≤Feb. 1991
89-C23	M	yearling	.940		14 Jul 1989	18 May 1991	MM 297 111	associated with C04 in 1989
89-C24	M	pup	.919		08 Aug 1989	17 May 1991	ML 361 933	pup of C17
89-C25	M	pup	.838		11 Aug 1989	21 Mar 1990	MM 098 145	pup of C17; silent radio-collar
89-C26	M	pup	.497		16 Aug 1989	8-9 Jan 1990	MM 113 156	apparent roadkill
89-C27	F	yearling	.576		17 Aug 1989	18 May 1991	MM 225 184	mortality sensor may 'stick'
89-C28	M	yearling	.277		18 Aug 1989	Autumn 1989	MM 141 183	shot
89-C29	F	yearling	.698		25 Aug 1989	≤16 Feb 1990	MM 052 194	slipped off radio-collar
89-C30	M	pup	.798		26 Aug 1989	Autumn 1989	MM 148 116	human-caused death; likely shot
89-C31	M	adult	.879		26 Aug 1989	06 Dec 1990	MM 132 158	visual- single; at a carcass
90-C67	M	yearling	.497		17 Mar 1990	20 Feb 1991	MM 188 129	visual- single
90-C68	F	adult	.638		24 May 1990	01 Mar 1992	MM 158 153	mate of C22 in 1990
90-C69	F	yearling	.621		05 Jul 1990	~21 Nov 1990	~LM 155 985	trapped ('Seech' area)
90-C70	M	pup	.598		22 Aug 1990	Jan 1991	MM 117 179	trapped; pup of C19 or C31

[1] pup (<9 months of age); yearling (9-21 months); adult (>21 months)

APPENDIX 3

SUMMARY OF TESTS OF INDEPENDENCE OF LOCATIONS FOR COYOTES MONITORED IN WINTER AND SUMMER DURING THE STUDY PERIOD

Table A3-1. Test of independence of observations (n) using *t*-tests for radio-collared coyotes tracked in winter, 1989-1990 in southwestern Manitoba, based on *t*-tests. Six time periods are used as a minimum time span between successive observations for each test. Schoener's (1981) ratio (modified by Swihart and Slade 1985b) compares the mean squared distance between successive observations (t^2) to the mean squared distance of each observation from the center of activity (r^2). Theoretically, a t^2/r^2 value of 2.0 is expected when all observations are statistically independent of each other. Standard deviations (S.D.) of t^2/r^2 are calculated from nonconsecutive observations and assuming a normal distribution of t^2/r^2. Statistical independence of locations is indicated for $\alpha = 0.05$ (**) or $\alpha = 0.25$ (*). Because the tested hypothesis is that locations are independent, an $\alpha = 0.25$ would reduce the probability of committing a type II error, hence minimum times for independence are usually greater than those for $\alpha = 0.05$.

	>4 Hours		>8 Hours		>12 Hours		>16 Hours		>20 Hours		>24 Hours	
COYOTE[1]	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)
C04-w90	1.3972	0.1309 (142)	1.6328	0.1505 (106)	1.7588 **	0.1695 (84)	1.8619 *	0.1862 (68)	1.8941 *	0.1912 (63)	1.9007 *	0.1981 (57)
C04-w89	1.0692	0.1602 (100)	1.1841	0.1667 (91)	1.5389	0.1909 (69)	1.5757	0.1958 (63)	1.5048	0.2014 (61)	1.7565 **	0.2237 (52)
C07	0.3050	0.1805 (77)	0.3465	0.1904 (68)	0.3752	0.2103 (55)	0.4424	0.2220 (50)	0.4748	0.2237 (47)	0.5368	0.2487 (37)
C08	1.4923	0.1826 (73)	1.5299	0.1868 (69)	1.8074 **	0.1951 (61)	1.8262 **	0.2026 (57)	1.8193 **	0.2083 (54)	2.0491 *	0.2194 (46)
C11	1.0483	0.1551 (97)	1.2384	0.1603 (89)	1.4677	0.1827 (67)	1.3173	0.1905 (61)	1.4968	0.1948 (59)	1.4616	0.2242 (45)
C17-w90	1.3638	0.1447 (150)	1.5996	0.1675 (112)	1.8636 **	0.1821 (92)	1.9595 *	0.2112 (72)	1.8866 *	0.2082 (66)	2.3188 *	0.2157 (61)
C17-w89	1.4254	0.1789 (81)	1.4439	0.1842 (76)	1.7458 **	0.2008 (61)	1.8687 *	0.2079 (55)	1.9108 *	0.2179 (51)	1.7712	0.2450 (42)

Table A3-1. (continued).

	>4 Hours		>8 Hours		>12 Hours		>16 Hours		>20 Hours		>24 Hours	
COYOTE[1]	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)
C20-w89	0.2468	0.2846 (46)	0.2468	0.2846 (46)	0.2674	0.3174 (37)	0.2694	0.3311 (34)	0.2928	0.3355 (33)	0.3234	0.3692 (27)
C20-w90	1.0092	0.1847 (93)	1.0698	0.2154 (67)	1.3590	0.2279 (57)	1.6757 **	0.2614 (43)	1.6940 **	0.2717 (40)	1.7123 **	0.2830 (37)
C21	1.4859	0.1285 (150)	1.7392	0.1497 (109)	1.8821 **	0.1560 (92)	1.7667 **	0.1747 (72)	1.6594	0.1798 (67)	1.9423 *	0.1859 (60)
C22	1.4813	0.1319 (154)	1.7083	0.1564 (111)	1.6045	0.1679 (90)	2.0738 *	0.2004 (71)	2.0540 *	0.2056 (64)	2.2910 *	0.2202 (60)
C23	0.5457	0.1267 (132)	0.7047	0.1473 (97)	0.7628	0.1614 (80)	0.9252	0.1788 (65)	0.9987	0.1881 (58)	1.1107	0.2003 (54)
C31	0.9745	0.1206 (147)	1.1766	0.1441 (105)	1.2306	0.1604 (85)	1.4843	0.1699 (72)	1.7331 **	0.1934 (60)	1.4410	0.2016 (55)

[1] w90 = winter 1990; w89 = winter 1989

Table A3-2. Test of independence of observations (n) using *t*-tests for radio-collared coyotes tracked in summer, 1989-1990 in southwestern Manitoba. Six time periods are used as a minimum time span between successive observations for each test. Schoener's (1981) ratio (modified by Swihart and Slade 1985b) compares the mean squared distance between successive observations (t^2) to the mean squared distance of each observation from the center of activity (r^2). Theoretically, a t^2/r^2 value of 2.0 is expected when all observations are statistically independent of each other. Standard deviations (S.D.) of t^2/r^2 are calculated from nonconsecutive observations and assuming a normal distribution of t^2/r^2. Statistical independence of locations is indicated for $\alpha = 0.05$ (**) or $\alpha = 0.25$ (*). Because the tested hypothesis is that locations are independent, an $\alpha = 0.25$ would reduce the probability of committing a type II error, hence minimum times for independence are usually greater than those for $\alpha = 0.05$.

	>1 Hour		>3 Hours		>6 Hours		>12 Hours		>18 Hours		>24 Hours	
COYOTE[1]	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)	t^2/r^2	S.D. (n)
C04	1.2322	0.0899 (340)	1.6007	0.1087 (224)	1.6643	0.1214 (177)	1.4582	0.1520 (117)	1.3170	0.1737 (89)	1.3626	0.1959 (75)
C17	1.3082	0.1281 (177)	1.5713	0.1362 (146)	1.5864	0.1472 (125)	1.6040	0.1742 (88)	1.5310	0.1940 (70)	1.5899	0.2064 (62)
C22	1.2309	0.1015 (233)	1.8376 **	0.1348 (128)	1.9712 *	0.1465 (110)	1.9382 *	0.1691 (78)	2.1387 *	0.1907 (61)	2.2458 *	0.2110 (50)
C22 seq	1.2238	0.1140 (180)	1.8953 **	0.1515 (98)	2.0757 *	0.1781 (72)	2.0878 *	0.2123 (49)	2.3012 *	0.2528 (35)	2.0645 *	0.2848 (27)
C68	1.3728	0.1009 (228)	1.8036 **	0.1353 (123)	2.0150 *	0.1491 (96)	1.8218 **	0.1853 (67	2.0942 *	0.2081 (50)	1.7438 **	0.2375 (42)
C68 seq	1.5323	0.1485 (102)	2.0047 *	0.2081 (50)	1.9698 *	0.2417 (38)	2.0701 *	0.3175 (23)	2.2790 *	0.4032 (16)	1.5923 **	0.4242 (13)

[1] sequential sampling period (June and July) only.

APPENDIX 4

DESCRIPTION OF ACTIVITIES AT CARCASS SITES ESTABLISHED FOR COYOTES DURING SUMMER SOUTH OF RIDING MOUNTAIN NATIONAL PARK, MANITOBA, 1989-90.

Few studies have investigated the role of food supply in coyote ecology (*e.g.*, Clark 1972, Hoffman 1979, Mills and Knowlton 1991). However, these studies have only considered the influence of the winter food supply while ignoring the summer season, probably because summer is considered a time where food is relatively abundant. Except for wolves (Mech 1977), winter has been the period that food stress is thought to occur while summers should yield abundant prey for predators. Consequently, summer food studies of coyotes seem only to document what coyotes have eaten during this period. However, denning adult coyotes faced with feeding a litter of 4-6 pups or more may exact a demanding role of provider for the parents, at least during some periods. Carbyn (1989) suggested this possibility to explain the increased aggression to humans by coyotes in July. Pups, at this time, may be in transition from relying on adults for food to acquiring food on their own. Consequently, July may be the time of greatest nutritional stress for denning adults and must therefore increase their foraging activity to meet this demand. Because adult coyotes may spend about half their time attending pups until these pups are at least nine weeks of age (Harrison 1983, Harrison and Gilbert 1985), foraging effort may require much of the remaining time. If foraging efficiency were increased for denning adult coyotes. more time would be available and presumably directed to pup attendance. Therefore if food could be added and utilized by denning coyotes, an increase in den attendance might be expected.

Consequently, I provided food supplements to an experimental group of coyotes and compared it with a control group where no food was added. Ungulate carcasses comprised the main source of food supplements although smaller mammals such as beavers (*Castor canadensis*) and porcupines (*Erithizon dorsatum*) were used whenever available. I placed carcasses near (<500m) confirmed or suspected den/rendezvous sites of monitored coyotes in woodlots that allowed ground vehicle access. Vehicle access minimized human scent left at the carcass when carcass sites were checked or resupplied. Where feasible, I setup a remote camera surveillance system (Telonics, Mesa, Arizona) at the carcass sites in an effort to document all visitors.

Initially, female coyote C17 received food supplements in 1989 while female coyote C04 acted as the control. However, no coyote activity was observed at two carcass sites near C17's den site, so two carcass sites were established near C04's den sites instead. Although the first deer carcass was consumed by coyotes after five days, a black bear (*Ursus americanus*) was responsible for subsequent feedings at this first site and a second site established later near C04's relocated den site. In 1990, I added food to two sites on the home range of C68 (female) and mate C22. The first carcass at site #1 was completely consumed within one week but consumption by coyotes could not be confirmed. A second carcass site was established 650m from site #1, but was decomposing with insect larvae before being consumed by a carnivore, likely a bear. Coyotes did consume a deer carcass overnight when it was placed near a suspected rendezvous site (adult female C19) immediately outside RMNP in late August 1990. These coyotes had inhabited areas inside RMNP until then.

My addition of food to some coyote home ranges had no measurable impact on their movements. Although the actual amount of food added was inadequate to influence behavior over the denning period, this was because carcasses would only be added after a previous one was consumed. Although some carcasses were eaten by coyotes, others were taken by bears or decomposed by insects. Coyotes visited food addition sites irregularly and apparently only used a carcass if they discovered the carcass soon after I introduced it. Otherwise, as decomposition progressed, the carcass apparently became more suitable for bears. Consequently, no significance was attibuted to these sites and were ignored. Therefore, baiting techniques intended for coyotes in summer may be plaqued with difficulties and fail. Supplementing food in winter avoids some of the inherent difficulties of warm temperatures and should be more successful. A chronology of events that occurred at each introduced food sites is presented below.

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Table A4.1. Carcass sites (A & B) established on the home range of adult female coyote C17 during summer 1989.

DATE	COMMENTS
25 May	→ Placed a 12.5 kg (27.5 lbs.) frozen beaver carcass at carcass site A (MM 095.5 150.0) → C17 den site (at MM 086.0 152.0) located about 900m away
28 May	→ First indication that C17 den site may have been moved (likely due to human disturbance)
29 May	→ Added 28.6 kg (63 lbs.) white-tailed deer (WTD) carcass to site A
30 May	→ No activity observed at carcass site → Carcass eventually consumed by insect larvae etc.
06 June	→ Added 49.6 kg (109 lbs.) WTD carcass near C17 den site #3 (near MM 081 152) at carcass site B (MM 080.5 151.5) → Actual den site not located then to avoid den disturbance and possible den site relocation
13 June	→ No coyote activity observed at carcass site B → Retrieved WTD carcass at carcass site B and refroze for later use with coyote C04 as the experimental unit

Total Weight Of Carcass Pieces Added = 90.7 kg (both sites)

Table A4.2. Carcass sites (A & B) established on the home range of adult female coyote C04 during summer 1989.

DATE	COMMENTS
15 June	→ Placed a 49.6 kg (109 lbs.) frozen white-tailed deer (WTD) carcass at carcass site A (MM 194.0 127.0) approx. 150m from the estimated den site (MM 193 129)
16 June	→ No activity observed at carcass site A
19 June	→ WTD carcass visited; pieces of fur pulled out (might be ravens but no feces observed)
21 June	→ WTD carcass completely consumed; only skeleton and hair left → 3 major feeding sites found; likely coyotes (radio-locations implicate coyote C04 presence here)
22 June	→ Placed another frozen WTD carcass (48 kg) at carcass site A
23-25 June	→ No activity observed at WTD carcass
26 June	→ Small black bear observed approx. 550m from WTD carcass site
28 June	→ WTD carcass consumed with 2 feeding sites found but skeletal remains were missing (and never were found)
29 June	→ Placed a third frozen WTD carcass (58.6 kg) at carcass site A
30 June	→ WTD carcass fed on but most of carcass remains untouched
03 July	→ WTD carcass gone and bear paw prints visible on truck left at site (therefore assume carcass was eaten by a bear)
16 July	→ Placed a porcupine carcass (~5 kg) at carcass site B (MM 184.0 110.0) approx. 200m from the estimated location of coyote C04's newly relocated den/rendezvous site (~MM 183 109) → Added a WTD carcass (estimated at 45 kg) to carcass site B (bloated condition of the road-killed deer precluded an acurate weight measurement)
19 July	→ WTD carcass untouched → Porcupine carcass decomposed from maggotts → Placed a 20 kg bag of dog food adjacent to WTD carcass
24 July	→ Only ribs and hair remained from WTD carcass; dog food bag moved, ripped open, & split → Remote camera pictures showed a bear at WTD carcass → Black bear observed approx. 250 m from carcass site B

Table A4.2 (continued)

DATE	COMMENTS
28 July	→ Placed a reindeer carcass (81.4 kg) at carcass site B (reindeer obtained from a local game farmer)
01 August	→ No coyote activity observed at carcass site B yet → Remote camera pictures showed turkey vultures present on the carcass
07 August	→ Reindeer carcass completely decomposed → Food addition stopped

Total Weight Of Carcass Pieces Added = 307.6 kg (est.)
(both sites)

Table A4.3. Carcass sites (A &B) established on the home range of adult female coyote C68 and her male mate C22 during summer 1990.

DATE	COMMENTS
19 June	→ added a white-tailed deer (WTD) carcass (34 kg without head and lower legs) to carcass site A (MM 155.0 150.5)
21 June	→ dragged a porcupine carcass (4 kg) from all-terrain vehicle from C68's den area to carcass site A
01 July	→ WTD carcass completely consumed; → WTD hair trail extends about 90m and carcass dragged over logs; therefore likely consumed by a black bear → porcupine carcass missing → discontinued carcass site because of suspected bear presence
16 July	→ added a 50 kg WTD carcass to carcass site B (MM 160.0 155.0)
19 July	→ no activity observed at carcass site B
22 July	→ decomposition of WTD evident (site B)
28 August	→ WTD at site B now completely decomposed → 1 coyote scat found at site

Total Weight Of Carcass Pieces Added = 88 kg (both sites)

APPENDIX 5

DESCRIPTION OF ACTIVITIES AT CARCASS SITES ESTABLISHED FOR COYOTES DURING WINTER SOUTH OF RIDING MOUNTAIN NATIONAL PARK, MANITOBA, 1988-89 and 1989-90.

Table A5.1. Carcass site W17a (MM 116.0 158.0) established near the periphery of the home range of adult female coyote C17 during winter 1988-89.

DATE	COMMENTS
12 January	→ 1 domestic cow carcass placed here by landowner → Carcasses estimated at 295 kg (650 lbs.) → Occasional visits by coyotes noted by tracks in snow
18 January	→ Captured adult female coyote C19 at trail leading into carcass site
24 January	→ Cow carcass eaten left front leg & part of left side of ribs (left side of carcass is exposed) → Part of left side of neck was eaten
mid-February	→ 2 domestic calf carcasses added (each carcass is estimated at 23 kg) → 1 domestic cow carcass (partially consumed by coyotes) relocated to here from landowner's barnyard about 300m away → No further consumption of partially eaten domestic cow or calf carcasses by coyotes
23 February	→ Removed newborn domestic calf carcass estimated at 12 kg (half-eaten by coyotes) from the landowner's barnyard (calf was thought to be born 21 Feb.)
26 February	→ 2 sets of coyote tracks entered trail leading into cow carcass site
05 March	→ The head of the domestic cow moved overnight by coyotes to the access road about 50m away
07 March	→ Thawed (but unskinned) white-tailed deer carcass (49 kg) introduced & immediately consumed by coyotes overnight (coyote C19 & mate observed in the area)
>08 March	→ No further significant consumption of the cattle carcasses by coyotes

Total Weight Of Carcass Pieces Added = 402 kg (estimated)

Table A5.2. Carcass site W17b (MM 095.5 150.0) established near the periphery of the home range of adult female coyote C17 during winter 1988-89.

DATE	COMMENTS
19 February	→ White-tailed deer (WTD) carcass (43 kg) thawed & introduced to carcass site
20/21 February	→ No coyote activity at the carcass site
22 February	→ Added a second WTD carcass (75 kg field-dressed) to site → Coyote tracks nearby but not at carcass site
23 February	→ Raven droppings at WTD carcasses → 1 raven observed when carcasses checked → 2 sets of coyote tracks observed on trails near the carcass site but not at the carcasses themselves
24 Feb - 03 Mar	→ No coyote activity evident at WTD carcasses
04 March	→ Male coyote C11 observed running from woodlot containing the deer carcasses when the site was approached by snowmobile
09 March	→ WTD carcasses remained untouched by coyotes
12 March	→ WTD carcasses fed on by coyote(s); many tracks
17 March	→ Some chewing noted on hind end of the small WTD carcass
22 March	→ Both WTD carcasses completely consumed; pictures taken

Total Weight Of Carcass Pieces Added = 118 kg

Table A5.3. Carcass site W4a (MM 193.5 132.0) established in the central portion of the home range of adult female coyote C04 during winter 1989-90.

DATE	COMMENTS
12 January	→ Activated carcass site with 2 carcass pieces → total weight = 38 kg
14 January	→ Added 1 carcass piece (17 kg)
15 January	→ Began intensive monitoring
19 January	→ Coyote tracks observed on snowmobile trail but tracks veered off before the carcass site
23 January	→ Added remains (36.5 kg) of cow elk carcass abandoned by hunters & consumed by coyotes elsewhere → No coyote activity observed; just ravens
28 January	→ Coyote activity at carcass site; some feeding occurred on the domestic cow leg → Might have been only 1 coyote involved
01 February	→ Added 1 carcass piece (29.5 kg) → Coyote tracks observed on snowmobile trail & at carcass but no good evidence for any feeding
07 February	→ Only raven activity observed at carcass site → 1 single coyote track observed nearby (~100m)
11 February	→ No apparent coyote activity noted except a single coyote track ~50m from the carcass site
18 February	→ No coyote activity observed; just ravens & possibly a weasel
21 February	→ No coyote activity observed
23 February	→ No coyote activity observed
27 February	→ No coyote activity observed
25 March	→ Coyote tracks observed at carcass → Cow elk carcass remains dragged ~10m from original site → Added 2 more carcasses pieces total weight = 22.0 kg
05 April	→ Nothing consumable left of carcass; just bones & 'capes'
09 April	→ No coyote activity observed

Total Weight Of Carcass Pieces Added = 143 kg

Table A5.4. Carcass site W4b (MM 181.5 140.0) established in the central portion of the home range of adult female coyote C04 during winter 1989-90.

DATE	COMMENTS
15 February	→ Activated carcass site with a white-tailed deer (WTD) carcass (45 kg) → Coyote tracks observed on snowmobile trail leading up to carcass site & a second set of coyote tracks observed through the woodlot to the site → Therefore coyotes were aware of the trail & have used it
18 February	→ No coyote activity observed; just ravens
21 February	→ Coyote tracks observed on snowmobile trail → Right hind quarter carcass piece chewed
27 February	→ WTD carcass consumed; just a rumen left → No skeletal remains found
28 February	→ Added second WTD carcass to site → weight estimated at 50 kg
03 March	→ Coyote tracks observed nearby but not at carcass; only raven sign at carcass
07 March	→ Some feeding occurred at rear of WTD carcass
17 March	→ WTD carcass completely consumed → Added another carcass piece (34.5 kg)
18 March	→ Discovered a doe fawn WTD carcass (during aerial relocation) virtually all consumed (MM 177.0 149.0) → Coyotes C04, C23, & 1 other (C04's mate?) aerially observed nearby
25 March	→ 3 sets of coyote tracks observed near carcass site → Raven activity (crows too?) → Added 3 more pieces; total wt. = 42.0 kg
05 April	→ Some coyote activity noted at carcass
07 April	→ Added a bloated WTD carcass (est. ~60 kg) to site
09 April	→ Carcass site visited by a wolf but no feeding occurred

Total Weight Of Carcass Pieces Added = 231.5 kg (estimated)

Table A5.5. Carcass site W4c (MM 211.0 141.0) established near the periphery of the home range of adult female coyote C04 during winter 1989-90.

DATE	COMMENTS
15 February	→ Activated carcass site with a white-tailed deer (WTD) carcass total weight = 79 kg
20 February	→ Coyote & possibly red fox tracks observed up to carcass site → Part of carcass fed upon but likely only by ravens
23 February	→ Old canid tracks present (coyote?)
27 February	→ Coyote & wolf tracks observed at carcass site → WTD carcass physically gone → 2 wolf scats collected
28 February	→ 2 sets of coyote tracks observed on trail to carcass site → Added a 2nd WTD carcass (56 kg)
03 March	→ Coyote tracks observed leading to carcass → Some feeding but may have been from ravens
07 March	→ Extensive feeding by coyotes has occurred but some usable parts still remain
17 March	→ WTD carcass vitually consumed in its entirety → No recent sign observed → Therefore, consumption was before snowstorm (15 Mar) → Added another carcass piece (49.5 kg)
25 March	→ Coyote tracks observed at carcass → WTD virtually all consumed → Added a domestic cow head (9 kg) to carcass site → Remains of elk leg found out in adjacent field
05 April	→ No coyote activity likely since 25 Mar (cow head untouched)

Total Weight Of Carcass Pieces Added = 193.5 kg

Table A5.6. Carcass site W22a (MM 152.5 162.5) established in the central portion of the home range of adult male coyote C22 during winter 1989-90.

DATE	COMMENTS
12 January	→ Activated carcass site with 2 pieces total weight = 33 kg
14 January	→ Pair of coyote tracks passed woodlot containing the carcass site but no tracks observed at carcass itself
15 January	→ Began intensive radio-tracking
19 January	→ Coyote tracks observed on snowmobile trail but the tracks veered off before the carcass site
23 January	→ Added the remains of a cow elk carcass abandoned by hunters & consumed by coyotes (remains comprised mostly bones and hide totalling 40 kg) → 1 pair of coyote tracks observed following snowmobile trail up to carcass site but then continued through the woodlot as if to avoid the carcass → Therefore, these coyotes likely knew of the carcass site but were wary of it
26 January	→ No indication of coyote activity observed; just 2 ravens
01 February	→ Added 1 carcass piece (12.5 kg) → 2 sets of coyote tracks observed on snowmobile trail → No coyote tracks observed at carcass site; just activity from raven and a hare evident
03 February	→ No coyote activity observed; just ravens
07 February	→ No coyote activity observed at carcass site but some tracks bypassed the woodlot (as before)
11 February	→ 1 set of coyote tracks observed on snowmobile trail leading to carcass site but the tracks left the trail ~150m before the carcass site → Raven activity continued → Coyotes seem to have avoided the carcass so far
16 February	→ Coyote tracks observed on snowmobile trail up to the carcass site → Carcass possibly fed on by coyotes but may still be only from ravens

Table A5.6. (continued)

DATE	COMMENTS
01 March	→ Coyote tracks observed entering into woodlot where carcass site was located but tracks stopped short of carcass
03 March	→ No coyote activity observed
13 March	→ No consumption of carcass by coyotes was evident but 1 set of coyote tracks observed nearby → Track of smaller mammal (likey skunk or raccoon) observed at carcass → Raven sign was evident as usual
25 March	→ Coyote tracks observed at carcass → Coyotes dug through snow to get at partially covered carcass pieces but not much feeding evident, if any

Total Weight Of Carcass Pieces Added = 85.5 kg (estimated)

Table A5.7. Carcass site W22b (MM 155.5 150.5) established in the central portion of the home range of adult male coyote C22 during winter 1989-90.

DATE	COMMENTS
16 February	→ Coyote tracks were prevalent on snowmobile trail & at the area where the carcass was to be introduced → Activated carcass site with a white-tailed deer (WTD) carcass (65 kg)
18 February	→ 1005 hrs- Coyote observed at carcass site by T. Sallows - Coyote C22 signal originated from sighting → 1504 hrs- Carcass visited by at least 1 coyote - Ravens have fed on carcass but coyotes may not have yet
27 February	→ WTD carcass virtually all consumed → Added second WTD carcass (59 kg) & turned over first carcass remains to increase carcass availability/use
01 March	→ About 12 ravens observed (by binoculars) at carcass site → When carcass was visited later, about 24 ravens flew away → Coyote tracks observed at carcass site → Some feeding occurred on carcass but likely all by ravens
03 March	→ Coyote activity (tracks) observed at carcass; also raven tracks observed throughout
07 March	→ 2 WTD carcasses virtually consumed → Added another carcass piece (40 kg)
13 March	→ Virtually nothing left to eat on carcass; just parts of skeletal column → Added 4 more carcass pieces (total wt = 70.5 kg)
25 March	→ Some carcass consumption by coyotes → Skunk observed at carcass → Added 3 more carcass pieces (total wt = 63.0 kg)
05 April	→ Only 1 domestic cow leg left intact
10 April	→ Coyote sign at carcass but feeding was not evident

Total Weight Of Carcass Pieces Added = 243.5 kg

Table A5.8. Carcass site W27a (MM 226.0 177.0) established near the periphery of the home range of yearling/adult female coyote C27 during winter 1989-90.

DATE	COMMENTS
12 January	→ Activated carcass site with 2 carcass pieces → total weight = 35 kg
14 January	→ Added another carcass piece (20 kg) → No tracks observed at the carcass site
15 January	→ Began intensive monitoring
16 January	→ No coyote activity observed at the carcass site
18 January	→ No coyote activity observed at the carcass site → A coyote was observed at MM 220.5 182.0
25 January	→ No coyote activity observed at the carcass site
28 January	→ No coyote activity observed at the carcass site; just ravens
31 January	→ Coyote track observed on snowmobile trail which lead to the carcass site but abruptly reversed its direction ~50m before the carcass site → Therefore, the coyote was wary of the carcass site
03 February	→ No coyote activity observed at the carcass site
04 February	→ No coyote activity observed at the carcass site → An elk/moose gut pile at MM 229.0 181.5 → likely shot 2-3 days ago → coyote & raven tracks were present at the gut pile
07 February	→ No coyote activity observed at the carcass site but 1 set of small canid tracks observed on snowmobile trail
11 February	→ No coyote activity observed at the carcass site
20 February	→ Many coyote tracks observed at the carcass site → likely 1 or 2 coyotes were that visited repeatedly
21 February	→ Coyote tracks observed leading into the carcass site
22 February	→ Added a whole domestic heifer carcass to carcass site → estimated weight at ~250 kg
23 February	→ No recent coyote activity observed at the carcass site
25 February	→ Coyote tracks observed up to the carcass site → Some feeding occurred on the separate leg piece

Table A5.8. (continued)

DATE	COMMENTS
01 March	→ No coyote activity observed since last check; just ravens
05 March	→ Coyote tracks observed at the carcass site → heifer carcass untouched but separate domestic cow legs appeared eaten → Flipped over the heifer carcass to expose the other side
07 March	→ Some coyote activity observed at the carcass → Last leg piece was gone
17 March	→ Only raven activity observed at the carcass site
19 March	→ Single coyote track observed leading to carcass site → Some consumption evident
20 March	→ No recent coyote activity observed since the previous day
24 March	→ Single coyote track observed at the carcass but the track continued on past the carcass site → No major feeding on carcass evident, if any
30 March	→ No further activity observed, if any, from coyotes

Total Weight Of Carcass Pieces Added = 305 kg (estimated)

APPENDIX 6

LETTER OF PERMISSION FOR PREVIOUSLY COPYRIGHTED MATERIAL

Jan 13/92

Dear Mr Cliff:

You have my permission to use the coyote drawing in conjunction with your thesis; under the conditions you stated. I hold all distribution rights to my work, so there is no problem in your using it.

Good luck, on your thesis

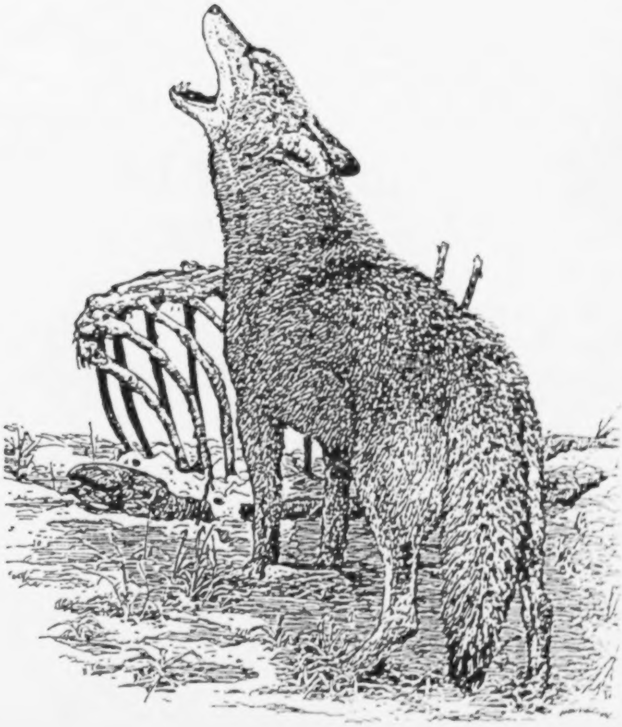
Sincerely,

Bill Haussecker.

COYOTE

THE ARTIST

Born in 1932, Bill Haussecker is a self-taught artist. He presently occupies a lot of his time teaching adult painting and sketching classes throughout southeastern Saskatchewan. His works have led to several awards in competitions and exhibitions.



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07 January 1992

Bill Haussecker
Box 53
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Dear Mr. Haussecker,

I am graduate student (M.Sc.) here in the Zoology Department conducting my M.Sc. research on coyotes. I expect to be completing my thesis sometime this April.

I have seen your pen-and-ink drawing of the coyote at a carcass and thought that this would complement my thesis about coyotes, their movements, and the influence of their food supply.

In my studies, I added carcasses to certain areas of their home range and monitored the effect on radio-collared coyotes in the area. Consequently, your drawing captures the essence of my thesis and I would appreciate your permission (and publishers, if necessary) to include a copy of this print in my thesis.

The thesis is considered an unpublished document but I expect to make about 30-50 copies for free distribution to libraries, research institutions, and individuals. In no way would I profit financially from your drawing while there would be some exposure of your talent to those who may see the thesis.
I hope that my request is acceptable and look forward to hearing from you. Thank you very much for your time and consideration.

Sincerely,

H. Dean Cluff